BOTANY

Volume LXXXV Number 3

UNIV. OF NEBR.
MAY 24 1928
LIBRARY

The BOTANICAL GAZETTE

FOUNDED BY JOHN M. COULTER

MAY 1928

Studies in Onagraceae. II - - - - - - Philip A. Munz 233

Respiration of the Soy Bean - - - - - - A. L. Hafenrichter 271

Revision of the Genus Bejaria mutis
B. Fedtschenko and N. Basilevskaja 299

Anatomy of Lycopodium Sporeling - Earle Augustus Spessard 323

Water-Solubility of Dry Matter in Relation to Calcium Nutrition of Normal Orange and Lemon Leaves - - A. R. C. Haas 334

Overcoming Delayed Germination of Nelumbo lutea James A. Jones 341

Stimulating Effect of Amino Acids on Sugar Metabolism of Plant and Animal Cells
W. E. Burge, G. C. Wickwire, A. M. Estes, and Maude Williams 344

Current Literature
Book Reviews - - - - - - - - - - - - 348
Notes for Students - - - - - - - - - - - - 352

THE UNIVERSITY OF CHICAGO PRESS
CHICAGO, ILLINOIS, U.S.A.

THE CAMBRIDGE UNIVERSITY PRESS, London
THE MARUZEN COMPANY, LIMITED, Tokyo
THE COMMERCIAL PRESS, LIMITED, Shanghai

Volume LXXXV Number 3

THE BOTANICAL GAZETTE

A JOURNAL EMBRACING ALL DEPARTMENTS OF BOTANICAL SCIENCE

Editors

HENRY CHANDLER COWLES
JOHN MERLE COULTER, Emeritus

Associate Editors

CHARLES JOSEPH CHAMBERLAIN, Morphology
MERLE CROWE COULTER, Genetics
SCOTT VERNE EATON, Physiology
GEORGE DAMON FULLER, Ecology
EZRA JACOB KRAUS, Applied Botany
WILLIAM JESSE GOAD LAND, Morphology
GEORGE KONRAD KARL LINK, Pathology
ADOLPH CARL NOÉ, Paleobotany
EARL EDWARD SHERFF, Taxonomy
CHARLES ALBERT SHULL, Physiology

Issued May 19, 1928

The Botanical Gazette is published in eight issues annually (omitting January and February, and July and August) by the University of Chicago at the University Press, 5750 Ellis Avenue, Chicago, Ill. ¶The subscription price is $9.00 per year; the price of single copies is $1.25. Orders for service of less than a half-year will be charged at the single-copy rate. ¶Postage is prepaid by the publishers on all orders from the United States, Mexico, Cuba, Porto Rico, Panama Canal Zone, Republic of Panama, Dominican Republic, Canary Islands, El Salvador, Argentina, Bolivia, Brazil, Colombia, Chile, Costa Rica, Ecuador, Guatemala, Honduras, Nicaragua, Peru, Hayt, Uruguay, Paraguay, Hawaiian Islands, Philippine Islands, Guam, Samoan Islands, Balearic Islands, and Spain. ¶Postage is charged extra as follows: For Canada and Newfoundland, 30 cents on annual subscriptions (total $9.30); on single copies 4 cents (total $1.29); for all other countries in the Postal Union, 60 cents on annual subscriptions (total $9.60), on single copies 8 cents (total $1.33). ¶Patrons are requested to make all remittances payable to The University of Chicago Press in postal or express money orders or bank drafts.

The following are authorized to quote the prices indicated:

For the British Empire: The Cambridge University Press, Fetter Lane, London, E.C. 4, England. Yearly subscriptions, including postage, £2 8*s*. each; single copies, including postage, 6*s*. 8*d*. each.

For China: The Commercial Press, Limited, Paoshon Road, Shanghai. Yearly subscriptions, including postage, $9.60; single copies, including postage, $1.33, or their equivalents in Chinese money.

Claims for missing numbers should be made within the month following the regular month of publication. The publishers expect to supply missing numbers free only when losses have been sustained in transit and when the reserve stock will permit.

Business correspondence should be addressed to The University of Chicago Press, Chicago, Ill.

Communications for the editor and manuscripts should be addressed to the Editor of the BOTANICAL GAZETTE, The University of Chicago, Chicago, Ill.

Contributors are requested to write scientific and proper names with particular care, to use the metric system of weights and measures, and in citations to follow the form shown in the pages of the BOTANICAL GAZETTE.

Papers in excess of thirty-two printed pages are not accepted unless the author is willing to pay the cost of the additional pages, in which case the number of the pages in the volume is correspondingly increased. Carbon copies of manuscripts will not be accepted.

Illustrations are furnished without cost to author only when suitable originals are supplied. Plates in excess of four are not accepted unless the author is willing to bear the additional cost. A copy of the suggestions made in the April number, 1916, will be sent on application. It is advisable to confer with the editors as to illustrations required in any article to be offered.

Separates, if desired, must be ordered in advance of publication. A table showing approximate costs of separates is printed on an order blank which accompanies the proof; a copy will be sent on request.

Entered as second-class matter August 21, 1896, at the Post-Office at Chicago, Illinois, under the Act of March 3, 1879.

Acceptance for mailing at special rate of postage provided for in Section 1103, Act of October 3, 1917, authorized on uly 15, 1918.

PRINTED IN THE U.S.A.

Selective Fertilization

By
DONALD F. JONES

Selective fertilization is here dealt with in a manner that will be of interest to every biologist. Dr. Jones discusses in detail those factors operating in the plant and animal world which influence the exercise of choice in mate selection. This book brings together the results of the investigations carried on at the Connecticut Agricultural Experiment Station on unequal fertilization and aberrant ratios which have been published in the *Biological Bulletin*, *Science and Genetics*.

This book constitutes the first successful compilation of material bearing upon the subject. Particularly significant to the biologist are chapters dealing with sterility within species, sterility among species, assortative mating, and with the question of physiological isolation in evolution. Dr. Jones is one of the leading investigators along these lines and his book has an important bearing upon the problems of both biology and botany.

$2.00, postpaid $2.10

THE UNIVERSITY OF CHICAGO PRESS
CHICAGO . . . ILLINOIS

General Cytology

A Textbook of Cellular Structure and Function

For Students of Biology and Medicine

Edited by E. V. COWDRY

The first co-operative and comprehensive attempt by specialists in research fields to state in general terms what is known or conjectured regarding the principles which govern cellular structure and function. It is the first volume to present the data concerning the cell that are fundamental not only to the sciences of botany and zoölogy, but also to physiology and pathology.

Thirteen eminent scientists have contributed to its preparation: Robert Chambers, E. G. Conklin, E. V. Cowdry, M. H. Jacobs, E. E. Just, Margaret R. Lewis, W. H. Lewis, Frank R. Lillie, Ralph S. Lillie, C. E. McClung, A. P. Mathews, T. H. Morgan, and E. B. Wilson. Each has written on that part of the subject which has occupied his own research, and the result is a more comprehensive and authoritative presentation of cytology than has ever before been attained.

Royal 8vo, 754 pages, illustrated, $7.50, postpaid $7.75

THE UNIVERSITY OF CHICAGO PRESS
CHICAGO . . . ILLINOIS

Rhus Dermatitis

Its Pathology and Chemotherapy

By JAMES B. McNAIR

¶ The lack of any rational treatment for the common infection resulting from poison oak or poison ivy has suggested a protracted study of the isolated principle, in the hope that knowledge of its characteristic properties may serve as a basis for such treatment.

¶ Complete analysis of cause, effect, and remedy has been attained by investigating from the three distinct standpoints of pharmacology, botany, and chemistry.

$4.00, postpaid $4.15

The University of Chicago Press
Chicago - - - Illinois

METHODS IN PLANT HISTOLOGY

Fourth Edition

By Charles Joseph Chamberlain

So extensive have been Professor Chamberlain's revisions that he has given us practically a new book. Re-written throughout, it brings up to date the methods for preparing all kinds of plant structure for microscopic study. New illustrations have been added, and more attention has been given to collecting material, and to recognizing and preserving the forms found in one's own neighborhood.

Methods in Plant Histology may be used in classes under an instructor, but the directions are explicit, and now, more than ever, it will help the student working alone learn to make first-class preparations.

$3.25, postpaid $3.37

The University of Chicago Press
Chicago · Illinois

The Anatomy of Woody Plants

By E. C. JEFFREY

Jeffrey, the leading authority on plant anatomy, is the most original investigator in this field since the great DeBary. This is a standard work on the subject—the only recent book to compare with DeBary's classic.

It does for the anatomy of plants what has long been done for human anatomy. Paleobotanical evidence figures largely, and the book is equally valuable to the paleobotanist, the morphologist, and the general student.

"Its value as a textbook in the anatomy of woody plants is of signal importance."—*Scientia.*

Illustrated $4.75, postpaid $4.87

THE UNIVERSITY OF CHICAGO PRESS
CHICAGO · ILLINOIS

The University of Chicago Science Series

The following volumes are bound uniformly in maroon cloth, small 12mo.

The Evolution of Sex in Plants. By JOHN MERLE COULTER. x+140 pages. $1.25, postpaid $1.35.

Individuality in Organisms. By CHARLES MANNING CHILD. x+212 pages. $1.50, postpaid $1.65.

The Origin of the Earth. By THOMAS C. CHAMBERLIN. xii+272 pages. $2.00, postpaid $2.10.

Finite Collineation Groups. By HANS F. BLICHFELDT. xii+194 pages. $1.50, postpaid $1.60.

The Biology of Twins. By HORATIO HACKETT NEWMAN. x+186 pages. $1.50, postpaid $1.60.

The Physiology of Twinning. By HORATIO HACKETT NEWMAN. x+232 pages. $1.75, postpaid $1.85.

Food Poisoning. By EDWIN OAKES JORDAN. viii+116 pages. $1.25, postpaid $1.35.

The Electron: Its Isolation and Measurement, and the Determination of Some of Its Properties. By ROBERT ANDREWS MILLIKAN. xiv+294 pages. $2.00, postpaid $2.10.

The Living Cycads. By CHARLES JOSEPH CHAMBERLAIN. xiv+172 pages. $1.50, postpaid $1.60.

Problems of Fertilization. By FRANK R. LILLIE. xii+278 pages. $1.75, postpaid $1.85.

The Origin and Development of the Nervous System from a Physiological Viewpoint. By CHARLES M. CHILD. xviii+296 pages. $1.75, postpaid $1.85.

The Story of the Maize Plant. By PAUL WEATHERWAX. xvi+248 pages. $1.75, postpaid $1.85.

The Antiquity of Disease. By ROY L. MOODIE. xiv+150 pages. $1.50, postpaid $1.60.

Algebras and Their Arithmetics. By LEONARD E. DICKSON. xii+242 pages. $2.25, postpaid $2.35.

Protoplasmic Action and Nervous Action. By RALPH S. LILLIE. xiv+417 pages. $3.00, postpaid $3.10.

Studies in Optics. By A. A. MICHELSON. 176 pages. $2.00, postpaid $2.10.

Selective Fertilization. By DONALD F. JONES. 163 pages. $2.00, postpaid $2.10.

THE UNIVERSITY *of* CHICAGO PRESS
CHICAGO · ILLINOIS

THE NATURE OF THE WORLD AND OF MAN

By Sixteen Members of the Faculty of the University of Chicago

In its new edition this book will continue to serve as a most important factor of the success of the survey course that directs the college Freshman toward the proper orientation to the world and man as science sees them. A completely revised chapter and minor revisions throughout the book appear in this new edition. These changes have been made as a result of additional classroom use, of helpful suggestions from those using the text, and of advances in various fields. Frequent revision to keep this book abreast of the best educational practice is an important factor in the plan upon which it is based.

The Critics Say—

"One of the finest and most engrossing popularizations of current science in existence. . . . . It is simple, clear, concrete, reliable. One emerges from it the richer by solid information and definite concepts."—HENRY HAZLITT, *New York Sun.*

"A manual of the physical and biological sciences of which it would be hard to speak too highly. The volume is so many things that an outline ought to be but frequently is not. It is selective in the sense of plucking the real heart out of a body of data."—*The New York Times Book Review.*

MERLE C. COULTER
"The Evolution of the Plant Kingdom"

"For the story is well told, well illustrated, and well colored with human significance. Certainly the volume is accurate; the names of the various contributors guarantee that. Certainly it is interesting and readable, and popular without being diluted."—*The Nation.*

HENRY C. COWLES
"Interactions between Plants and Their Environments"

$4.00, postpaid $4.15

THE UNIVERSITY OF CHICAGO PRESS
CHICAGO - - - ILLINOIS

VOLUME LXXXV NUMBER 3

THE
BOTANICAL GAZETTE

May 1928

STUDIES IN ONAGRACEAE[1]

II. REVISION OF NORTH AMERICAN SPECIES OF SUBGENUS SPHAEROSTIGMA, GENUS OENOTHERA

PHILIP A. MUNZ

For this study there have been available almost 2000 sheets of herbarium material, which have come from the following collections, the abbreviation given in each case being that used in citing specimens: University of California (C), Herbarium of Frank Peirson of Pasadena (FP), Gray Herbarium of Harvard University (G), Missouri Botanical Garden, special material (M), Pomona College (P), Stanford University (S), United States National Herbarium, special material (US), University of Wyoming (W), Washington State College (WS). These herbaria have been visited or material has been borrowed from them. To those in charge of these collections, and especially to Dr. B. L. ROBINSON of the Gray Herbarium, I am much indebted for courtesies shown. I wish also to express appreciation to Dr. I. M. JOHNSTON of the Gray Herbarium for many kindnesses, and to Dr. H. M. HALL of the Carnegie Institution, to Director A. W. HILL of the Kew Botanical Garden, to Professor L. DIELS of Berlin, and to Dr. CARL CHRISTENSEN of Copenhagen for notes on and photographs of types.

In so far as this paper represents the results of a study of a part of a group on which more extensive work is under way, it may be considered as a preliminary revision. Up to the present time I have had access to insufficient South American material for any adequate

[1] No. 1 of this series appeared in Amer. Jour. Bot. 15: 223–240. 1928.

study of the species of that region, although in one or two cases I have seen fit to use South American specific names for North American plants. Until opportunity is offered for a more thorough study of the southern species I shall not be ready for a discussion of phylogeny. So far as I can make it do so, the key expresses my present idea of relationship among the species.

Subgenus Sphaerostigma (Seringe) JEPSON, Man. Calif. 680. 1925.

Sphaerostigma as sect., Seringe, in DC., Prodr. **3**:46. 1828; as genus, F. & M., Ind. Sem. Hort. Petrop. **2**:49. 1835. *Chamissonia* as genus, Link, Jahrb. Gewaechsk. 186. 1818. *Chamissonia* Endlicher, Gen. 1190, in syn., 1840. *Agassizia* as genus, Spach, Hist. Veg. Phan. **4**:347. 1835. *Holostigma* as genus, Spach, Nouv. Ann. Mus. Paris (III) **4**:332. 1835.

Calyx tube obconic to linear-funnelform; stamens subequal to distinctly unequal, and in 2 sets, all fertile; stigma capitate; capsule sessile or subsessile, cylindrical or narrowed toward tip, terete or quadrangular, usually curved or contorted; usually annual, with simple leaves; flowers white or yellow, often turning red or green on drying.

The application of Article 49 of the International Rules makes it necessary to use the name *Sphaerostigma* rather than *Chamissonia*.

KEY TO SPECIES

Flowers white (yellowish in *minor* and in 2 vars. of *decorticans*), often drying pinkish; borne in terminal spikes

Capsules cylindrical, terete, linear, not thickened in lower portion, scarcely if at all coiled, not noticeably attenuate at tip

Petals 5–7 mm. long, suborbicular; style exceeding corolla, 10–13 mm. long; calyx tube 4–6 mm. long; capsules refracted or spreading, occasionally coiled.—Deserts from S. Utah to Ariz. and S. California ..... 1. *O. refracta*

Petals 3 mm. long, spatulate; style shorter than corolla, 3.5–4 mm. long; calyx tube 2.5–3 mm. long; capsules divaricately spreading.—Deserts from W. Texas to S. Utah and S. California ..... 2. *O. chamaenerioides*

Capsules not strictly cylindrical, but somewhat enlarged near base and attenuate at tip

Mature capsules usually distinctly contorted and coiled, not merely bent and curved, quite slender, not subfusiform in shape (see also *O. decorticans* var. *desertorum*)

Flowers minute; petals 1–2 mm. long, narrowly obovate; style 1.5–3 mm. long; calyx tube 1–2 mm. long; longer filaments almost twice as long as shorter....3. *O. minor*

Flowers larger; petals 3.5–5 mm. long, orbicular-ovate; style 6–12 mm. long; calyx tube 3–8 mm. long; filaments subequal

Flowers and leaves arranged in spicate tufts at ends of naked prostrate branches or on short central stalk; capsules 10–12 mm. long, conspicuously quadrangular.—Extreme W. Nevada.....4. *O. nevadensis*

Flowers and leaves continuous from base of stems, not in terminal tufts; capsules 14–23 mm. long, not conspicuously quadrangular.....5. *O. alyssoides*

Mature capsules merely curved or bent, not distinctly contorted nor coiled, subfusiform in shape

Leaves largely near base, glabrate, lance-ovate to oblanceolate; stems glabrous or glabrate, with epidermis exfoliating promptly; capsule 15–25 mm. long; seeds ash-colored and linear-obovoid.....6. *O. decorticans*

Leaves well distributed, glandular-pubescent to glandular-villous, ovate to oblong-ovate; stems glandular-pubescent to glandular-villous; epidermis exfoliating tardily, if at all; capsule 10–15 mm. long; seeds brownish, rhomboid-prismatic.....7. *O. boothii*

Flowers yellow, often drying greenish, borne in axils of foliage leaves

Capsules terete, cylindrical or subfusiform, but not quadrangular; leaves narrow, 1–4 mm. wide, usually linear-oblong

Plants with several naked, fine, often capillary stems, each bearing leafy inflorescence at tip; capsule subfusiform, almost straight, 5–8 mm. long.—E. Washington to E. California and to Wyoming.....8. *O. andina*

Plants with stems leafy from base; capsules terete, straight or coiled, 15–40 mm. long

Flowers small; petals 2.5–3.5 mm. long; calyx lobes 1.5–3.5 mm. long.....9. *O. contorta*

Flowers larger; petals 5–15 mm. long; calyx lobes 3–12 mm. long.....10. *O. dentata*
Capsules quadrangular; leaves 5–20 mm. wide, lanceolate to ovate
Mature capsules oblong-pyramidal, 12 mm. long, nearly straight.—Guadalupe Island.....11. *O. guadalupensis*
Mature capsules curved or contorted, 15–40 mm. long
Flowers small; petals 1.5–7 mm. long.....12. *O. hirta*
Flowers larger; petals 8–22 mm. long
Plants of sea bluffs and inland; greenish (except for a desert form); cauline leaves lanceolate to lance-ovate, acute, wavy-margined, thin.....13. *O. bistorta*
Plants of sea beaches, grayish to silvery (except in var. *nitida*); cauline leaves lance-oblong to orbicular-ovate, obtuse, not wavy-margined, thick..14. *O. cheiranthifolia*

Description of species

1. Oenothera refracta S. Wats., Proc. Am. Acad. **17**:373. 1882.—Leveille, Monogr. Oenoth. 210. 1905; *Sphaerostigma refractum* (S. Wats.) Small, Bull. Torr. Bot. Club **23**:192. 1896; Nels., Bot. Gaz. **40**:58. 1905; *Oenothera deserti* Jones, Contr. West. Bot. **12**:15. 1908; *Sphaerostigma deserti* (Jones) Heller, Muhlenbergia **9**:68. 1913.

Annual, 15–40 cm. high, erect, with few to several divaricately spreading branches, usually glandular-puberulent and somewhat strigillose throughout; stems slender, commonly dark red, becoming whitish in age and with epidermis exfoliating; leaves largest near base of plant, but well distributed up to lowest flowers, oblanceolate to lanceolate to oblong-linear, entire or remotely and shallowly denticulate, green or slightly reddish, with callous tip, blades 20–50 mm. long and 3–8 mm. wide, lowest narrowed into petioles 10–20 mm. long, upper subsessile, uppermost reduced to linear bracts; inflorescence racemose, sometimes paniculate, 5–15 cm. long; calyx tube linear-funnelform, 4–6 mm. long, finely pubescent within; calyx lobes lance-oblong, 5–6 mm. long, often reddish; petals suborbicular, 4–7 mm. long and 3.5–6 mm. wide, whitish; stamens almost as long as petals, longer filaments 3.5–4.5 mm. long, shorter ones scarcely 1 mm. less; anthers 2–2.5 mm. long, pale yellow; style pubescent in

lower half, 10–13 mm. long, exceeding corolla; stigma about 1 mm. wide; capsule linear, commonly refracted or spreading, and straight or curved, sometimes coiled, 30–50 mm. long, about 0.5 mm. thick, generally not conspicuously beaked; seeds pale, linear, 1 mm. long.

Type locality (first specimen cited), "first collected by BIGELOW near the Colorado." Ranging on the deserts from Southern Utah to Arizona and Southern California. Representative material: UTAH, Bear Valley, *Palmer* 165 (G, NY): NEVADA, Hole-in-the-Rock, *Jones* 5036r (P); Rhyolite, *Jones* in 1907 (P); Bunkerville, *Jones* 5027 (P); Gold Mt., *Purpus* 5993 (C); Moapa, *Goodding* 2205 (C, G, W,); Las Vegas, *Goodding* 2239 (G, W); Overton, *Heller* in 1912 (S): ARIZONA, Chimehuevis, *Jones* in 1903 (P); Beaverdam, *Jones* 5024q (P); Ft. Mohave, *Cooper* in 1860–61 (G); Grand Canyon, *Gray* in 1885 (G); gravelly hills in the Colorado, *Bigelow* in 1854, type coll. (G, NY); Parker, *Wooton* in 1913 (US): CALIFORNIA, near Bishop, *K. Brandegee* in 1913 (C); Inyo, *T. S. Brandegee* in 1891 (C); Funeral Mts., *Jones* in 1907 (P); Cave Spring, *Jones* in 1924 (P); Kelso, *Jones* in 1906 (P); Daggett, *Parish* 9778 (C, S); Newberry, *Munz* et al. 4190 (P); Needles, *Jones* in 1884, type *O. deserti* (C, P); Chuckwalla Mts., *Munz* & *Keck* 4916 (P); Salton, *Hall* 5840 (C, S); Dos Palmos Spring, *Munz* 9947 (P); San Felipe Creek, *Eastwood* 2753a (G).

2. OENOTHERA CHAMAENERIOIDES Gray, Pl. Wright. **2**:58. 1853. —*O. chamaenerioides* Gray, in Wats. Proc. Am. Acad. **8**:593. 1873; Leveille, Monogr. Onoth., 229. 1905, in part; *Sphaerostigma chamaenerioides* (Gray) Small, Bull. Torr. Bot. Club **23**:189. 1896; *S. erythrum* Davidson, Bull. Soc. Calif. Acad. **1**:118. pl. IX. 1902; *Oenothera erythra* (Davidson) Macbride, Contrib. Gray Herb **65**:41. 1922.

Erect annual, 1–5 dm. high, usually branching near base; stems slender, often reddish, lower portions of stem and branches glandular-puberulent, somewhat viscid, upper portion more or less finely strigillose- or glandular-puberulent; leaves rather thin, bright green, sometimes reddish, glabrate, blades of basal ones ovate-lanceolate to lanceolate, 4–8 cm. long, 1–2.5 cm. wide, entire, obtuse at apex, gradually attenuate at base with narrowly winged petioles 1–3.5 cm. long; lower cauline leaves somewhat reduced, upper ones below inflorescence becoming subsessile, those of inflorescence reduced to acute linear bracts, 10–20 mm. long; inflorescence a simple corymbose raceme, elongating in fruit and becoming as much as 20 cm. long; calyx tube narrowly funnelform, 2.5–3 mm. long, pubescent within; calyx lobes lance-ovate, 2.5 mm. long; petals white, often

drying pinkish, spatulate, ca. 3 mm. long; stamens subequal, glabrous; filaments almost 2 mm. long; anthers oblong, about 1 mm. long; style 3.5–4 mm. long, shorter than petals, pubescent on lower half; stigma 1 mm. wide; capsule terete, linear, divaricately spreading, scarcely if at all beaked, 25–50 mm. long, 0.5 mm. thick; seeds pale, linear, about 1 mm. long.

Type locality, near El Paso, Texas; ranging from there westward to California and Utah; growing only in deserts. Representative material: TEXAS, El Paso, *Jones* 3751 (C, P), *Wright* 1377, type (G); Frontera, *Bigelow* 373 (NY): SONORA, bed of Rio de Sonora, *Rose, Standley* & *Russell* 12413 (US): ARIZONA: Clifton, *Davidson* 244, type coll. *O. erythra* (C); Phoenix, *Jones* in 1903 (P); Tucson, *Thornber* 508 (C); Nogales, *T. S. Brandegee* in 1892 (C); Yucca, *Jones* 3934 (P, W); Wickenberg, *Jones* in 1903 (P); Beaverdam, *Jones* 5024 r (P): UTAH, Dugway, *Jones* in 1891 (P); St. George, *Jones* 1623 (C, G, NY, P, W); southern Utah, *Parry* 71 (G, NY): NEVADA, Truckee Pass, *Kennedy* 1307 (W); Rhyolite, *Jones* in 1907 (P); Empire City, *Torrey* 100 (G); Calientes, *Jones* in 1904 (P): CALIFORNIA, Pleasant Canyon, Panamints, *Hall* & *Chandler* 6964 (C, P); Shepherd's Canyon, *Jones* in 1897 (P); Daggett, *K. Brandegee* in 1914 (C); Keyes Ranch, *Jones* in 1927 (P); Needles, *Munz* & *Harwood* 3632 (P); Goffs, *Jones* in 1903 (P); Chuckwalla Mts., *Munz* & *Keck* 4853 (C, P); Palm Canyon, *Spencer* 1465 (P); Mt. Springs Grade, *Peirson* 2898 (FP, P); San Felipe, *T. S. Brandegee* in 1895 (C); Yaqui Well, *Jones* in 1926 (P): LOWER CALIFORNIA, El Llano de Santana, *T. S. Brandegee* in 1889 (C).

The reduction of *O. erythra* needs no comment; there are no characters separating *O. erythra* from *O. chamaenerioides*.

3. OENOTHERA MINOR (Nelson), n. comb.—*Sphaerostigma minus* (given as *minor*) Nelson, Bull. Torr. Bot. Club **26**:130. 1899.

Annual, more or less canescent-strigillose throughout (though leaves may be glabrate), scarcely if at all glandular; stems simple and erect or usually with several subequal ascending stems, somewhat reddish, slender, 5–30 cm. high, only tardily exfoliating; basal leaves largest, blades spatulate to oblanceolate to elliptic-ovate, subentire, acute to obtuse, 3–15 mm. wide, 5–25 mm. long, narrowed gradually into slender petioles 5–20 mm. long; upper leaves narrower and smaller, uppermost becoming linear-lanceolate foliose bracts; flowers borne singly in axils of almost all leaves, upper ones grouped in spicate inflorescence; calyx tube funnelform, 1–2 mm. long, pubescent within; calyx lobes narrowly ovate, 1–2 mm. long; petals "yellowish" to ochroleucous, often drying reddish, narrowly obovate,

1–2 mm. long; stamens strongly biseriate, the longer filaments twice the shorter ones and ca. two-thirds length of petals; anthers rounded, glabrous, 0.5–1.0 mm. long; style glabrous, almost equaling petals, 1.5–3 mm. long; stigma 0.5–1 mm. broad; capsule 10–25 mm. long, more or less contorted, gradually narrowed from base, often beaked; seeds narrowly obovoid, somewhat angled, grayish, ca. 1 mm. long.

KEY TO VARIETIES

Calyx tube 2 mm. long; calyx lobes and petals 2 mm.; capsules 18–25 mm. long; ranging from Wyoming to Nevada and Idaho....3a. *O. minor* var. *typica*

Calyx tube about 1 mm. long; calyx lobes and petals 1–1.2 mm; capsules 10–18 mm. long; Eastern Washington and Oregon....3b. *O. minor* var. *cusickii*

3A. OENOTHERA MINOR (Nelson) Munz var. **typica,** n. nom.—*Sphaerostigma minus* (given as *minor*) Nelson, l. c.; *S. nelsonii* Heller, Muhlenbergia **1**:1. 1900; Nelson, BOT. GAZ. **40**:57. 1905; *Oenothera alyssoides* var. *minutiflora* S. Wats., Bot. King Rep., 111. 1871; Proc. Am. Acad. **8**:591. 1873; *Sphaerostigma alyssoides* var. *minutiflorum* (S. Wats.) Small, Bull. Torr. Bot. Club **23**:192. 1896; *Sphaerostigma minutiflorum* (S. Wats.) Rydb., Bull. Torr. Bot. Club **33**:146. 1906; *Oenothera chamaenerioides* var. *torta* Leveille, Monogr. Onoth., 230. 1905, in part; *Sphaerostigma tortum* (Leveille) Nelson, BOT. GAZ. **40**:60. 1905; *S. tortum* var. *eastwoodae* Nelson, BOT. GAZ. **40**:61. 1905; not *Oenothera minutiflora* D. Dietr., Syn. Pl. **2**:1285. 1840; not *Sphaerostigma minutiflorum* F. & M., Ind. Sem. Hort. Petrop. **2**:50. 1835.

Calyx tube 2 mm. long; calyx lobes and petals 2 mm. long; style 3 mm., capsules 18–25 mm. long.

Type locality, Green River, Wyoming.—WYOMING, Ft. Steele, *Nelson* 3138 (W); Rock Springs, *Nelson* 9085 (W); Granger, *Nelson* 4691, type coll. *O. torta* (C, G, W); Green River, *Nelson* 4707 (P, W), 3047, type coll. *O. minor* (G, W), *Jones* in 1896 (P), *Payson* & *Armstrong* 3211 (P, W); Solon, *Williams* in 1897 (G): COLORADO, Grand Junction, *Eastwood* in 1892, type coll. var. *eastwoodae* (C, G, S): UTAH, Salina Canyon, *Jones* 5422i (P); Chepeta Well, *Jones* in 1908 (P); Milford, *Goodding* in 1902 (W), *Jones* in 1880 (P); Manti, *Jones* 5518 (C, P, W); Vermilion, *Jones* in 1901 (P); Hernansville, *Jones* in 1891 (P); Dutch Mt., *Jones* in 1891 (P), in 1900 (P); Black Rock, *Jones* 1958 (P), *Watson* 421 (G); Granite Mts., Tooele Co., *Jones* in 1900 (P): NEVADA, Shoshone, *Jones* in 1881 (P); Battle Mt., *Jones* in 1882 (P); Furber, *Jones* in 1891 (P); Oreana,

Jones in 1903 (P): IDAHO, Salmon, *E. B.* & *L. B. Payson* 1786 (G, W); Challis, *Macbride* & *Payson* 3233 (G, W).

In taking up the name *O. minor* for Watson's variety *minutiflora*, I am using the oldest species name for the concept, and am combining NELSON'S and LEVEILLE'S *torta* with *minor* (*Nelsonii* of HELLER). NELSON'S specimens of *minor* are somewhat immature, and do not have the characteristic spreading branches of older plants. A distinction is made also in flower color, being given as yellow for *minor* and white for *minutiflora*. Careful study has failed to reveal any morphological characters, and dried plants do not show any color characters. I am convinced that the small-flowered plants of Wyoming and adjacent regions form one concept which is amply distinct from *alyssoides* for specific rank, but not divisible into *minor* and *torta* and *eastwoodae*.

3B. OENOTHERA MINOR var. **cusickii,** n. var.—Smaller-flowered than var. *typica*, having calyx tube 1 mm. long; calyx lobes and petals 1–1.2 mm.; style 1.5 mm.; capsules 10–18 mm. long. (Tubus calycis 1 mm. longus; lobis calycis et petalis 1–1.2 mm. longis; capsulis 10–18 mm. longis.)

Type, Malheur River and adjacent hills, June 6, 1901, *W. C. Cusick* 2545 (University of California Herbarium 35348; cotypes at Gray, Pomona, and Wyoming): WASHINGTON, Moxee to N. Yakima, *Griffiths* & *Cotton* 41 (US); Coulee City, *Piper* 3889 (P, US, WS); Junction Crab & Wilson Creeks, *Sandberg* & *Leiberg* 262 (C, G, WS); Wilson Creek, *Sandberg* & *Leiberg* in 1893 (C); Morgans Ferry, Yakima River, *Suksdorf* 310 (G): OREGON, Malheur, *Cusick* 1223 (G), cited as 1228 by Leveille, Monogr. Onoth., 230, 1905 in his var. *torta;* Vale, Mathew Co., *Leiberg* 2051 (G); north end of Sumner Lake, *Eggleston* 6857 (US): IDAHO, Ft. Hall, *Coulter* in 1872 (US); a collection at Devil Creek, Owyhee Co., Idaho, by *Nelson* & *Macbride* 1747 (G, W) is intermediate between var. *cusickii* and var. *typica*. The variety *cusickii* has been included in *alyssoides* var. *minutiflora* and in *torta*.

4. OENOTHERA NEVADENSIS Kellogg, Proc. Calif. Acad. **2**:224. fig. 70. 1863.—*Sphaerostigma nevadense* (Kell.) Heller, Muhlenbergia **6**:51, with cover illustr., 1910; *Sphaerostigma tortuosum* Nelson, Proc. Biol. Soc. Wash. **17**:95. 1904; BOT. GAZ. **40**:61. 1905; *Oenothera gauraeflora* var. *vermiculata* Jones, Contr. West. Bot. **12**:16. 1908; *O. gauraeflora* var. *caput-medusae* Leveille, Monogr. Onoth., 226. 1905.

Annual, glabrate to finely and sparingly strigillose, especially on capsules, forming a small simple erect tuft, 2–5 cm. high, or in larger plants with several additional naked prostrate branches from 3–10 cm. long and each bearing a tuft or spike of leaves and flowers at the

tip; leaves narrowly oblanceolate, 10–35 mm. long, 3–7 mm. wide, glabrous, green, entire, not strongly veined, rounded or obtuse at apex, gradually narrowed at base to slender petioles 1–3 cm. long, or upper ones subsessile; uppermost reduced to leafy bracts; inflorescence spicate, usually crowded, sometimes elongate; calyx tube lance-ovate, sparingly pubescent, ca. 3 mm. long; petals white, orbicular-ovate, 3.5–5 mm. long; stamens in 2 series, the longer alternating with and equaling the petals, the shorter two-thirds as long; anthers oblong, 1.5 mm. long; style about 6 mm. long, equal to or slightly exceeding petals, glabrous; stigma 0.5 mm. broad; capsules 10–12 mm. long, 1.5–2 mm. thick, quadrangular with ridge running along middle of each of the four faces, swollen at base, gradually narrowed toward slender beak, coiled and twisted, usually in dense masses; seeds pale gray, ca. 1 mm. long, linear-obovoid.

Type locality not given. Ranging through Washoe and Ormsby counties in Nevada and possibly in adjacent California: NEVADA, hills north of Carson, *Stretch* in 1865 (NY); Wadsworth, *Kennedy* 2053 (S); Empire City, *Jones* 3862 (C, P, US, W), *no.* 4 (G); between Truckee Valley and Spanish Springs Valley, *Brandegee* & *Kennedy* in 1913 (C): Truckee Pass, *Kennedy* 766, type coll. *S. tortuosum* (C, S, W), 1592 (C), *Heller* 8647 (G, S); Reno, *Hillman* in 1894 (C), *Jones* in 1897, type coll. var. *vermiculata* (C, P, US), *Jones* in 1903 (P), *Cowgill* in 1901 (W), *Brandegee* (S), *Heller* 9697 (G, S): CALIFORNIA (?), *Lemmon* 102 (NY): fortunately the habit is so striking that good figures have been given with two of the names given to this plant, and specimens have been available for the others, so there is no question as to synonymy.

5. OENOTHERA ALYSSOIDES H. & A., Bot. Beechey Voy. 340. 1838.—Annual, usually branching from base, central stem erect, others ascending, and curved at tip, closely and finely pubescent throughout or short-villous especially at base, often glandular; stems rather slender, 5–35 cm. high, simple or again branched; lowest leaves oblanceolate to ovate-lanceolate, 15–40 mm. long, 5–15 mm. wide, entire or remotely denticulate, acute to obtuse, gradually narrowed into slender petioles of about same length; cauline leaves gradually reduced, subsessile; those of inflorescence still smaller, gradually becoming more bractlike; inflorescence racemose-spicate; calyx tube funnelform or sublinear, 3–8 mm. long; calyx lobes lance-ovate, 4–5 mm. long; petals white, 4–5 mm. long, orbicular-ovate; stamens glabrous, of two lengths, the longer ones somewhat shorter than the petals, with filaments 3.5 mm. long and anthers oblong and

1–1.5 mm. long; style 7–12 mm. long, equaling or slightly exceeding petals; stigma 0.5 mm. broad; capsule 14–23 mm. long, thickened at base (1.5 mm.), gradually attenuate toward beaklike tip, much coiled or only curved; seeds pale, linear-obovoid, minutely cellular-pitted.

KEY TO VARIETIES

Plant bright green in appearance, with only minute pubescence; calyx tube 2–3 mm. long, glabrous within; style glabrous; range in eastern Oregon and adjacent Idaho. . . . . 5a. *O. alyssoides* var. *typica*

Plant grayish in appearance, with conspicuous canescent or villous hairs; calyx tube 4–7 mm. long, pubescent within; style pubescent at base; from Utah to Nevada and Eastern California . . . . . 5b. *O. alyssoides* var. *villosa*

5A. OENOTHERA ALYSSOIDES H. and A. var. **typica,** n. nom.—*O. alyssoides* H. & A., l. c.; Hooker, Icones Pl., t. 339. 1841; Watson, Proc. Am. Acad. **8**:591. 1873, in part; *Sphaerostigma alyssoides* (H. & A.) Walp., Rep. **2**:78. 1843; Small, Bull. Torr. Bot. Club **23**: 1896, in part; Nelson, BOT. GAZ. **40**:62. 1905, in part; *Oenothera gauraeflora* of Leveille, Monogr. Onoth., 223. 1905, in part; *Sphaerostigma implexum* Nelson, BOT. GAZ. **52**:267. 1911.

General aspect of plant a bright green; pubescence of stems and leaves minute; flowers white, often drying yellowish; calyx tube 2–3 mm. long, glabrous within; style glabrous; capsules much coiled and twisted.

Type locality, "Pine Creek, Snake Country;" ranging in Eastern Oregon and adjacent Idaho: OREGON, desert region, E. Oregon, *Cusick* 1940 (G, WS); Malheur River, 40 miles above Ontario, *Griffiths* & *Morris* 899 (US); Mathew Valley, *Leiberg* 2257 (C, P, G); Ontario, *Leiberg* 2006 (C, G); base of Steins Mt., *Howell* in 1885 (C, G, WS); Old Ft. Smith, *Griffiths* & *Morris* 402 (US): IDAHO, Emmett, *Macbride* 890 (C, G, P, S, W); Falk's Store, Canyon Co., *Macbride* 27, type coll.; *S. implexum* (C, G, W, WS); King Hill, *Nelson* & *Macbride* 1098 (C, G, P, S, W); Glenns Ferry, *Jones* in 1911 (P); Weiser, *Jones* in 1899 (P): "CALIFORNIA," *Douglas* (G), probably type material, mislabeled as to locality and really from Snake Country.

As here restricted, *O. alyssoides* var. *typica* is much less inclusive than *O. alyssoides* usually is. Instead of using simply a villous condition to distinguish the var. *villosa*, I am using length of hypanthium, pubescence within the hypanthium, and pubescence on base of style, with a canescent pubescence on stems and leaves whether it be long or short. I have seen several intergrades, having styles weakly pubescent and hypanthium intermediate in length:

Nampa, Idaho, *Mulford* in 1892 (G); Humboldt Mts., Nevada, *Torrey* 99 (G); Humboldt River, *Beckwith* 33 (G); Summit Lake, N. Nevada, *Griffiths* & *Morris* in 1901 (US).

5B. OENOTHERA ALYSSOIDES var. VILLOSA S. Wats., Proc. Am. Acad. **8**:591. 1873.—*Sphaerostigma alyssoides* var. *macrophyllum* Small, Bull. Torr. Bot. Club **23**:192. 1896; Nelson, BOT. GAZ. **40**:62. 1905; *S. macrophyllum* (Small) Rydb., Bull. Torr. Bot. Club **40**:66. 1913; *S. utahense* Small, Bull. Torr. Bot. Club **23**:191. 1896; Nelson, BOT. GAZ. **40**:61. 1905; *Oenothera utahensis* (Small) Garrett, Spring Flora Wasatch Reg., 64. 1911; *O. gauraeflora* var. *hitchcockii* Leveille, Monogr. Onoth., 226. 1905; *Sphaerostigma hitchcockii* (Levl.) Nelson, BOT. GAZ. **40**:226. 1905.

With grayish aspect because of canescent or villous hair; flowers white, usually drying or aging pink; calyx tube usually 4–8 mm. long, pubescent within; style pubescent on lower half; capsules often merely curved.

Type locality, near Salt Lake, *Stansbury;* ranging to Nevada and the Mohave Desert of California: UTAH: Salt Lake Co., *Garrett* 1156 (G, W); Milford, *Jones* 1773 (P), *Goodding* in 1902 (W); north of Salt Lake City, *Rydberg* 6164 (W); near Salt Lake, *Stansbury*, type coll. (G, NY); Promontory Point, N. Utah, *Watson* 420 (G); Fish Springs, *Jones* in 1892 (P); Nephi, *Goodding* 1107 (G, W); Dugway, *Jones* in 1891 (P); Marysvale, *Jones* 5388f (P, US); S. Utah, *Parry* 68 (G); "Simpson's Park," July 6, 1859, type of *S. hitchcockii* (M): NEVADA, Trinity Mts. *Watson* 420 (G); Panaca, *Jones* in 1912 (P); Palisade, *Jones* in 1882 (P), *Stokes* in 1903 (US); Muncy, *Jones* in 1891 (P); Goldfield, *Tidestrom* 9764 (G); Currant, *Bentley* in 1916 (P, S, W); Good Springs, *Jones* in 1905 (P); Esmeralda Co., *Shockley* 324 (C, G); Pyramid Lake, *Kennedy* 2044 in part (C, S), *Tidestrom* 10668 (G): ARIZONA, Ft. Mojave, *Cooper* in 1860–1861 (G): CALIFORNIA, Amedee, *Jones* in 1897 (C); Lassen Co., *Eggleston* 7176 (US); Deep Springs Valley, *Ferris* 1357 (S); Silver Canyon, E. of Laws, *K.Brandegee* in 1913 (C, W); White Mts. E. of Laws, *Heller* 8238 (G, S, US); Benton, *Shockley* 113 (C).

As here used this variety is a rather comprehensive and variable concept. I am unable to divide it on the basis of leaf size or length of hair or on other characters that have been used. Typically it has the habit of *O. alyssoides* var. *typica*, that is, several spreading stems from the base and secund racemose spikes with lowest leaves oblanceolate and cauline ones lanceolate. Variants are as follows: (1) with stems single and branched above and usually slender and smooth as if from shade, the *Jones* collection at Fish Springs, Utah and at Good Springs, Nevada; (2) with cauline leaves becoming ovate and suggesting *O. boothii*, *Jones* 5388f, *Rydberg* 6164, *Jones* at Panaca and at Muncy, Nev.; (3)

with capsules less coiled and suggesting *O. decorticans*, part of the *Brandegee* collection from east of Laws; (4) with unusually long and villous hair, *Bentley* at Currant, Nev., *Goodding* and *Jones* collections at Milford, Utah.

6. OENOTHERA DECORTICANS (H. & A.) Greene, Fl. Francisc., 217. 1891.—Annual, erect, simple or branching below, and with branches ascending or spreading, glabrous or glabrate below, finely pubescent and often glandular in the inflorescence; stems with shining whitish or reddish epidermis which exfoliates readily; leaves largely near base, bright green or tinged red, glabrous to finely pubescent, lance-ovate to oblanceolate, entire or shallowly denticulate, acute, 2–8 cm. long, 0.5–3 cm. wide, narrowed into petioles of about same length; cauline leaves gradually reduced up the stem, becoming more narrow and subsessile; those of inflorescence reduced to lanceolate foliose or minute bracts; spikes usually fairly compact, in fruit 5–30 cm. long; calyx tube 4–6 mm. long, narrow, pubescent within; calyx lobes lance-ovate, 3.5–5 mm. long; petals white or reddish, obovate to suborbicular, 3.5–5.5 mm. long; filaments glabrous, not conspicuously unequal, almost as long as petals, anthers round-oblong to linear-oblong, 1–2 mm. long, glabrous; style almost equal to petals, pubescent on lower half; stigma about 0.5 mm. broad; capsule subfusiform, thickest in lower half, attenuate into slender beak, 1.5–3 mm. thick near base, 15–25 mm. long; seeds ash-colored, linear-obovoid, somewhat angled, minutely pitted, 1 mm. long.

KEY TO VARIETIES

Petals 3.5–4 mm. long, red, obovate, distinctly longer than wide; capsules curved with spreading tip; Mts. about western edge of Mohave Desert above 4000 ft. alt. ..... 6a. *O. decorticans* var. *rutila*

Petals over 4 mm. long, usually whitish, but liable to turn red in age

Capsules not over 2 mm. thick at base, not conspicuously quadrangular nor thickened and indurated at angles, scarcely woody; petals usually distinctly longer than wide; plants tall, 20–50 cm., and fairly slender

Fruits with simple curve about one-third from base, so that tips spread away from stem; base of capsule ca. 2 mm. thick; exfoliating epidermis of stem straw- or flesh-colored; Monterey and Stanislaus Counties, California, south to Los Angeles and Bakersfield ..... 6b. *O. decorticans* var. *typica*

Fruits often more contorted so that tips point down; base of capsules 1–1.5

mm. thick; epidermis of stem white; Mohave Desert east to Nye County, Nevada, and occasional on Colorado Desert

6c. *O. decorticans* var. *desertorum*

Capsules 3 mm. thick at base, conspicuously quadrangular and much thickened and indurated at angles and with additional less prominent shallow ridge on each face between the angles, quite woody; plants low and coarse, rarely over 15–20 cm. high; exfoliating epidermis white; petals suborbicular, about as wide as long; deserts from Victorville and Barstow, California, to St. George, Utah, and to Mexican boundary

6d. *O. decorticans* var. *condensata*

6A. OENOTHERA DECORTICANS var. **rutila** (Davidson), n. comb.—*O. rutila* Davidson, Erythea **2**:62. 1894; *Sphaerostigma rutilum* (Davidson) Parish, Erythea **6**:89. 1898; Nelson, BOT. GAZ. **40**:63. 1905.

Rather slender-stemmed, considerably diffused with red; flowers small; petals 3.5–4 mm. long, red, distinctly longer than wide; capsules as in var. *typica*.

Type locality, Big Rock Creek, San Gabriel Mts., Los Angeles County, California; an ill-defined variety ranging along desert side of San Gabriel Mts., and approached by material from Mt. Pinos and the Panamints, California; Big Rock Creek, *Davidson* in 1893, type collection (G, S), *Davidson* 1605, in 1906 (C, S), *Munz* 6829 (P); Lytle Creek, *Hall* 1474 (C, S): the following collections approach this variety: Mt. Pinos, *Hall* 6477 (C) with small flowers but not so red; Seymour Creek, Mt. Pinos, *Peirson* 3218 (P), *Munz* 6998 (P) with flowers somewhat larger and not so red; Griffins, *Elmer* 3734 (G) with small but less red flowers; Panamint Canyon, *Jones* in 1897 (P) with red but larger flowers; and Shepherds Canyon, *Jones* in 1897 (P) with larger and less red ones; I have not seen the *Coville* and *Funston* collections from the Panamints (Contr. U.S. Nat. Herb. **4**:105. 1893) listed under *O. gauraeflora* by COVILLE.

6B. OENOTHERA DECORTICANS (H. & A.) Greene var. **typica**, n. nom.—*Gaura decorticans* H. & A., Bot. Beechey, 343. 1838; *Oenothera decorticans* (H. & A.) Greene, Fl. Francisc., 217. 1891; *Sphaerostigma decorticans* (H. & A.) Small, Bull. Torr. Club **23**:191. 1896; Nelson, BOT. GAZ. **40**:60. 1905. *Oenothera alyssoides* var. *decorticans* (H. & A.) Jepson, Man. Calif., 686. 1925, in part; *Oenothera gauraeflora* T. & G., Fl. N. Am. **1**:510. 1840; Watson, Proc. Am. Acad. **8**:591. 1873; Leveille, Monogr. Onoth., 223. 1905, in part.

Rather large plants, commonly 30–50 cm. tall; exfoliating epidermis of stems not a dead white, but somewhat straw- or flesh-

colored; petals about 5 mm. long, distinctly longer than wide; capsules about 2 mm. thick near base, somewhat rounded in cross-section and with tips bending away from stems.

Type locality, Monterey; ranging along the coast from Monterey to Los Angeles counties and in the San Joaquin Valley: CALIFORNIA, without locality, *Douglas*, type material of *O. gauraeflora* and probably of *O. decorticans* (G); Corral Hollow, Alameda Co., *Brewer* 1218 (C, G); San Benito, *Dudley* in 1899 (S); Porcines, *Abrams* & *Borthwick* 7997 (S); Hernandez, *Lathrop* in 1903 (S); Paloma Creek, Monterey Co., *Ferris* 1945 (S); Soledad, *Ferris* 4143 (P, S); Mission Valley, *Hall* 10013 (C, G, W); San Antonio Canyon, *Brewer* 579 (C, G); Parkfield, *Munz* 9185 (P); Paso Robles, San Luis Obispo Co., *Barber* in 1899 (C, P, W), *Jones* in 1909 (P), *K. Brandegee* in 1911 (C), *Munz* 10120 (P); Santa Barbara Co., *Baker* in 1895 (C); Bardsdale, Ventura Co., *Hall* 3111 (C, P, W); Sespe Creek, *Abrams* & *McGregor* 176 (G, S); Bouquet Canyon, L. A. Co., *Munz* 10004 (P); Cuddy Canyon, Mt. Pinos, *Dudley & Lamb* 4505 (S) Gormans Station, *Dudley* & *Lamb* 4438 (P, S); Caliente Creek, *Munz* 8995 (P); Bakersfield, *Davy* 1784 (C); La Puerta Creek, *Elmer* 4372 (S); Greenhorn Range, *Hall* & *Babcock* 5093 (C); Alcalde, *T. S. Brandegee* in 1891 (C).

6c. OENOTHERA DECORTICANS var. **desertorum**, n. var.—Habit more slender than in var. *typica;* epidermis whiter; flowers as in *typica;* capsules more slender, 1–1.5 mm. thick at base, more contorted so that the tips often curve downward. (Cutis caulium alba; capsulis tenuibus, 1–1.5 mm. crassis basilare, contortis et deflexis.)

Type, 10 miles southwest of Garlic Springs, Mohave Desert, California, April 8, 1924, *Munz* & *Keck* 7881 (Pomona College Herb. no. 48926); ranging over the western half of the Mohave Desert into Owens Valley, California, and to Rhyolite, Nevada; occasional on the Colorado Desert of California: NEVADA, Rhyolite, *Heller* 9682 (G, S): CALIFORNIA, Palm Springs (Agua Caliente), *S. B.* & *W. F. Parish* 628 (C), *Jaeger* in 1925 (P); Victorville, *Munz* 2586 (S), *Jones* in 1903 (P); Rabbit Springs, *Parish* 4955 (S); Box S Ranch, *Jones* in 1926 (P); Barstow, *K. Brandegee* in 1915 (C), *Johnston* 6459 (P); Hesperia, *Abrams* 2170 (P, S); Muroc, *Peirson* 7271 (P); Lancaster, *Elmer* 3985 (G, P, S); Willow Springs, *F. Grinnell* 424 (US); Mohave, *Dudley* 515 (S); Randsburg-Rand, *K. Brandegee* in 1913 (C); Owens Lake, *Purpus* 1932 (C); Argus Mts., *Purpus* 5410 (C, G); Keeler, *Coville* & *Funston* 859 (G, S); Bissell, *K. Brandegee* in 1912 (C); Lone Pine, *Jones* in 1927 (P). In the Owens Valley var. *desertorum* grades insensibly into *O. alyssoides* var. *villosa*; on the whole it can be distinguished by its less contorted fruits, narrower petals, less pubescence, and by its tendency to have a central stalk instead of several stems from the very base as does *alyssoides*. Of the collections cited, however, *Coville* & *Funston* 859 and *Purpus* 5410 approach *O. alyssoides* var. *villosa*.

6D. OENOTHERA DECORTICANS var. **condensata,** n. var.—Stems low and thick, usually not over 15–18 cm. tall and with pure white epidermis; petals 4–5 mm. long, suborbicular; capsules woody, much thickened, about 3 mm. at base, quadrangular and with supplementary ridge down the middle of each face. (Caules crassi et 10–18 cm. alti; petalis 4–5 mm. longis, suborbicularibus; capsulis ligneis, circa 3 mm. crassis, quadrangularibus.)

Type, Dos Palmos Spring, Colorado Desert, Riverside County, California, Jan. 31, 1926, *Munz* 9960 (Pomona College Herb. no. 98708); ranging through the eastern half of the Mohave Desert and through the Colorado Desert, eastward to St. George, Utah: UTAH, S. Utah, *Parry* 67 (G); St. George, *Jones* in 1880 (P): NEVADA, Moapa, *Goodding* 2189 (C, G, W), *Jones* in 1904 (P); Mormon Mts., *Kennedy* & *Goodding* 128 (C); Good Springs, *Jones* in 1905 (P); Las Vegas, *Goodding* 2326 (W); Tuly's Ranch near Las Vegas, *Goodding* 2346 (G, W): ARIZONA, Cactus Station, *W. F. Parish* 66 (S); Valley of the Colorado, *Palmer* 135 (C); Stern's Ferry, *Jones* 5032c (P); Beaverdam, *Jones* 5024s (P): CALIFORNIA, Funeral Mts., *Jones* in 1907 (P); Randsburg-Rand, *K. Brandegee* in 1913 (C); Kelso, *Jones* in 1906 (P); Daggett, *K. Brandegee* in 1914 (C); Bagdad, *Munz, Harwood,* & *Johnston* 4291 (P); Needles, *Jones* 3787 (C, P, W); Blythe Junction, *Munz* & *Harwood* 3591 (P); Shavers Well, *Munz* & *Keck* 4747 (P); Chuckwalla Bench, *Hall* 5888 (C); Coachella, *Hall* 5804 (C); Palm Springs, *Spencer* 1445 (P); Signal Mt., *Abrams* 3174 (G, S); Borregos Springs, *K. Brandegee* in 1899 (C); Coyote Wells, *Spencer* 244 (G, P); Calexico, *Davy* 7993 (C). In describing this variety I admit that flowering material is somewhat difficult to distinguish, although the low habit of growth and the broad petals are fairly good characters. After the plants have somewhat mature capsules, however, they are very distinct. The thick woody stems with heavy capsules are quite persistent, and their dried remains are left standing on the desert for some time after the plant is dead, reminding one of a pine cone from which the scales have been broken and the shreddy scale bases and central axis are left.

7. OENOTHERA BOOTHII Dougl., ex Hook., Fl. Bor. Am. 1:213. 1834.—Annual, glandular-pubescent to glandular-villous throughout, erect, 1–4 dm. high, usually with central stem more prominent than the branches, which are few to several and spreading or ascending; leaves ovate or oblong-ovate, fairly evenly distributed, shallowly toothed, acute to obtuse, lowermost narrowed into petioles 1–3 cm. long, the blades 2–5 cm. long and 1–2.5 cm. wide; upper leaves gradually reduced and becoming sessile; those of inflorescence more or less foliose bracts; inflorescence racemose-spicate, often quite congested, elongating in fruit and becoming 5–15 cm. long; calyx

tube narrowly funnelform, 2–8 mm. long, pubescent within; calyx lobes lance-ovate, 2.5–7.5 mm. long; petals white, pinkish in age, clawed, obovate, 2.5–8.5 mm. long; stamens subequal; filaments glabrous, almost as long as petals; anthers rounded-oblong to linear, glabrous, 1–2 mm. long; style pubescent on lower half, 4–15 mm. long, equaling petals; capsules short, 10–15 (–18) mm. long, usually ascending in lower half and with terminal portion spreading but not contorted, much thicker at base (1.5–2 mm.) than in terminal portion; seeds brownish, rhomboid-prismatic, minutely cellular-pubescent, about 1 mm. long, immature seeds linear-obovoid, grayish.

KEY TO VARIETIES

Flowers small; petals 1.5–2.5 mm. long; Eastern Washington and Oregon. 7a. *O. boothii* var. *pygmaea*

Flowers larger; petals 3.5–9 mm. long; Idaho and S. E. Washington to Nevada and Eastern California ..... 7b. *O. boothii* var. *typica*

7A. OENOTHERA BOOTHII var. PYGMAEA (Dougl.) T. & G., Fl. N. Am. 1:510. 1840.–*O. pygmaea* Dougl., ex Lehmann in Hook., Fl. Bor. Am. **1**:213. 1834; *Sphaerostigma boothii* var. *pygmaeum* (Dougl.) Walp., Rep. **2**:78. 1843.

Flowers small; calyx tube 1.5–2.5 mm. long; calyx lobes 1.5–2.5 mm. long; petals 1.5–2.5 mm. long, narrowly obovate; style 4–5 mm. long.

Type locality, "near the branches of Lewis and Clark's River, lat. 46° north:" WASHINGTON, Rock Island, *Sandberg* & *Leiberg* 441 (C, G, P, WS): OREGON, Pine Creek, *Leiberg* 199 (C, G, US); Muddy Station, John Day Valley, *Howell* in 1885 (G, US, WS); Squaw Creek, *Henderson* 5411 (S). Photographs of the types of *O. boothii* and *O. pygmaea* Dougl. from the Kew Botanical Garden show that *O. boothii* has rather larger flowers, with petals about 3.5 mm. long, and the ovate merely serrate leaves of the more southern plants, which have largely gone under the name *Sphaerostigma senex*, and which commonly have petals ranging from 5 to 9 mm. long. The type of var. *pygmaea* has no flowers, but has the narrower and undulate-margined leaves of the smaller flowered plants of E. Washington and Oregon, and is quite like *Sandberg* & *Leiberg* 441. After careful comparison of these photographs with herbarium specimens of the larger and smaller flowered series, I refer the name *O. boothii* var. *pygmaea* to the latter, and *O. boothii* var. *typica* to the former.

7B. OENOTHERA BOOTHII Dougl. var. **typica,** n. nom.—*O. boothii* Dougl., ex Lehmann in Hook., Fl. Bor. Am. **1**:213. 1834; Watson,

Proc. Am. Acad. **8**:591. 1873, in part; *Sphaerostigma boothii* (Dougl.) Walp., Rep. **2**:77. 1843; Small, Bull. Torr. Bot. Club **23**:191. 1896, in part; Nelson, Bot. Gaz. **40**:61. 1905, in part; *Oenothera gauraeflora* race *boothii* of Leveille, Monogr. Onoth., 226. 1905, in part; *Sphaerostigma senex* Nelson, Proc. Biol. Soc. Wash. **18**:173. June 29, 1905; *S. lemmoni* Nelson, Bot. Gaz. **40**:61. July 18, 1905.

Flowers larger; calyx tube 4–8 mm. long; calyx lobes 3–7 mm.; petals 3.5–9 mm. long, broadly obovate; style 5–14 mm. long.

Type locality, "on the high sandy and gravelly hills of Lewis and Clark's River;" ranging from Eastern Washington to E. California and W. Nevada: Washington, Snake River, Walla Walla region, *Brandegee* 785 (C, G): Idaho, Shoshone Falls, *Henderson* in 1897 (W); Blue Lakes, *Palmer* 523 (US), 71 (US): those mentioned so far have flowers about the size of those in the type collection; the following are larger: Payette River, *Henderson* 3115 (US): Oregon, Snake River, *Nuttall* (G); Nevada, without locality, *Wheeler* in 1872 (US); Virginia Mts., *Bailey* 419 (G, US); Lake Range, *Watson* 419 (G, US); Walker Lake, *Heller* 10912 (C, G, S, US); Truckee Range, *Bailey* in 1867 (G); Carson Lake, *Peirce* in 1926 (P, S); Ely, *A. E. Hitchcock* 1198 (US); Pyramid Lake, *True* 750, type of *S. senex* (W); *K. Brandegee* & *Kennedy* in 1913 (C), *Frandsen* & *Brown* in 1906 (C, W), *Hall* 10554 (C); Candelaria, *Shockley* 324 (C, S); Gold Mt., *Purpus* 5901 (C, P); Austin, *Hitchcock* 744 (US): Utah: Diamond Valley, *Purpus* 6260 (C): Arizona, Cinder flats east of San Francisco Peaks, *Leiberg* 5808 (US); Francisco Mt., *Knowlton* 200 (US): California: East flank of Sierra Nevada, *Lemmon* 103, type of *S. lemmoni* (M), in 1875 (US); Hesperia, *Abrams* 2166 (S); upper part of Mojave River, *S. B.* & *W. F. Parish* 1504 (G, S).

This variety is exceedingly variable as to pubescence, size, leaf shape, etc., and it is sometimes difficult to distinguish from *O. alyssoides* var. *villosa*, but on the whole its capsules are shorter and not coiled, and the foliage is more decidedly glandular. Mature seeds are quite characteristic. Plants from about Pyramid Lake, Nevada, have especially large flowers.

8. Oenothera andina Nutt., ex T. & G., Fl. N. Am. **1**:512. 1840.—Low, erect, very slender-stemmed annuals, with very spreading branches from near the base or from above, finely canescent throughout, 2–15 cm. high and about as broad; lower stem and branches, in all except the smallest plants, rather free of leaves; leaves alternate, linear to oblanceolate-linear, entire, acute to obtusish at somewhat thickened apex, basally gradually attenuate into short indistinct petioles; blades 10–30 mm. long, 1–2.5 mm. wide, somewhat but not markedly reduced in upper part of plant, the upper ones rather crowded; flowers axillary in a rather crowded

corymb which becomes racemose in fruit; calyx tube 1–2 mm. long, sparsely pubescent; calyx lobes oblong-ovate, 1.5–2.5 mm. long; petals ovate to orbicular, sessile, 1.2–2.5 mm. long, yellow; stamens of 2 lengths, longer ones (including filaments) 1–2 mm. long, shorter ones about half as long; anthers 0.3–0.6 mm. long; style stout, 2.5–4.5 mm. long; stigma 0.4–0.7 mm. broad; capsules fusiform, somewhat quadrangular, 5–8 mm. long; seeds fusiform, smooth, brown, ca. 0.7 mm. long.

KEY TO VARIETIES

Flowers small; petals about 1.5 mm. long.....8a. *O. andina* var. *typica*
Flowers larger; petals about 2.5 mm. long.....8b. *O. andina* var. *hilgardii*

8A. OENOTHERA ANDINA Nutt. var. **typica,** n. nom.—*O. andina* Nutt., l. c.; Wats., Proc. Am. Acad. **8**:594. 1873; Leveille, Monogr. Onoth., 181. 1905; *Sphaerostigma andinum* (Nutt.) Walp., Rep. **2**:79. 1843; Small, Bull. Torr. Bot. Club **23**:188. 1896; Nelson, BOT. GAZ. **40**:56. 1905; *Oenothera andina* f. *tripetala* Leveille, l. c., 182.

Calyx tube about 1 mm. long; calyx segments 1.5 mm.; petals 1.5 mm. long, ovate; longer filaments 1. mm.; anthers 0.3 mm.; capsules 5–6 mm. long.

Type locality, "Dry plains in the Rocky Mountains, near the Black-Foot River." WYOMING: Cokeville, *Nelson* 4644 (G, W); Green River, *Parry* 111 (G, NY), *Payson* & *Armstrong* 3212 (P, W): UTAH, Heber Valley, *Watson* 425 (G, NY); Minersville, *Stokes* in 1903 (C): NEVADA, East Humboldt Mts., *Watson* 425 (G, NY); Havawat Mts., *Watson* 425 (NY); Empire City, *Jones* 3862 (C); Palisade, *Jones* 273 (P): IDAHO: Rocky Mts., *Nuttall,* type coll. (G, NY); Blackfoot, *Jones* in 1909 (C, P); Salmon, *E. B.* & *L. B. Payson* 1778 (G, W); Devil Creek, Owyhee Co., *Nelson* & *Macbride* 1746 (G, W); Squaw Creek, Boise Co., *Macbride* 806 (C, G, W); Tikura, *Nelson* & *Macbride* 1295 (C, G, P, W); Shoshone, *Mulford* in 1892 (NY); Weiser, *Jones* in 1899 (P); Pocatello, *Henderson* in 1897 (W): CANADA, Assiniboia, Pend d'Oreille Post, *Macoun* in 1895 (G); Medicine Hat, *Macoun* 7531 (G): WASHINGTON, Pasco, *Piper* 2994 (WS); Spangle. *Piper* in 1899 (WS); Omak, *Jones* in 1911 (C, P); Yakima, *Brandegee* in 1886 (G); Ellensburg, *Piper* 2675 (WS), *Elmer* 429 (P, WS); Wenatchee, *Whited* 86 (WS); Sprague, *Sandberg* & *Leiberg* 145 (C, G, WS); Klickitat Valley, *Howell* 1503 (C, NY, WS): OREGON, Steins Mts., *Howell* in 1885 (NY, WS); Baker City, *Jones* in 1902 (P); Chandlers Stage Station, *Eggleston* 6895 (US): CALIFORNIA, Goose Lake Valley, *Austin* in 1894 (C); Mt. Bidwell, *Manning* 384 (C); Shumway, Lassen Co., *Austin* & *Bruce* 2364 (C, S); Big Valley, Modoc Co., *Baker* & *Nutting* in 1894 (NY, C); Warners Mts., *Peirson* 6869 (P); Susanville, *Jones* in 1897 (P); Chat, *Jones* in 1897 (P).

8B. OENOTHERA ANDINA var. hilgardii (Greene), n. comb.—*O. hilgardi* Greene, Bull. Torr. Bot. Club **10**:41. 1883; *Sphaerostigma hilgardi* (Greene) Small, Bull. Torr. Bot. Club **23**:188. 1896; *S. andinum* var. *hilgardii* (Greene) Nelson, BOT. GAZ. **40**:56. 1905.

Flowers larger; calyx tube 1.5 mm. long; calyx lobes 2 mm.; petals 2.5 mm. long, suborbicular; longer filaments 2.0 mm.; anthers 0.6 mm.; capsules 7–9 mm. long.

Type locality, "moist alkaline soil of the Klickitat Swale, Washington:" WASHINGTON, without locality, *Whited* 1093 (US); Yakima Region, *Brandegee* in 1882 (C); Coulee City, *Piper* 3907 (WS); Ellensburg, *Whited* 388 (US); Wilson Creek, *Sandberg* & *Leiberg* in 1893, in part (W); Wenatchee, *Whited* 1093 (WS); Wenas, *Griffiths* & *Cotton* 89 (WS); Cascade Mts., *Vasey* in 1889 (WS); Jct. Crab & Wilson Creeks, *Sandberg* & *Leiberg* 290 (C, G, WS); Omak Lake, St. *John* 7698 (WS); Riverside, *St. John* 7706 (WS); Walla Walla region, *Brandegee* 786 (G); E. Wash. Territory, *Hilgard* in 1882, type coll. (G): OREGON, Hayden Island, Columbia River, *Nelson* 2948 (G).

This variety is marked as an entity mostly by its larger floral parts, and is not any too distinct. PIPER (Contr. U.S. Nat. Herb. **11**:405. 1906) recognizes var. *hilgardii* as a species, and distinguishes between it and *O. andina* on the basis of seeds as well as flower size, giving the seeds of the former as "pale, linear" and of the latter as "dark, clavate," a distinction I am unable to maintain. Furthermore, there is a certain amount of intergradation in flower size, as evidenced by the following collections which have petals about 2 mm. long: Wilson Creek, Wash., *Sandberg* & *Leiberg* in 1893, in part (C, P); Coulee City, *Piper* 3908 (WS); Juniper Springs, Mathew Co., Ore., *Leiberg* 2282 (C,G).

9. OENOTHERA CONTORTA Dougl. ex Hook., Fl. Bor. Am. **1**:214. 1834.—*Oenothera torulosa* Leveille, Monogr. Onoth., 176. 1905, in large part.

Annual, slender-stemmed, 5–40 cm. high, rarely simple, usually with few to several subequal branches from near the base, these erect or ascending; stems usually reddish, glabrate to pubescent, leafy; leaves linear to lance-linear or linear-oblanceolate, subsessile, remotely denticulate, glabrate to pubescent or short-villous, acute, 5–25 mm. long, 1–3 mm. wide; lower leaves frequently with fascicles of smaller ones in axils or with short branches; uppermost leaves reduced to leafy bracts subtending the flowers; flowers few to many on a stem, but only one or two in anthesis at once; calyx tube obconic, 1–2 mm. long, glabrous or pubescent within and glabrate to glandular or strigillose without; calyx lobes lance-ovate, 1.5–3.5

mm. long, varying in pubescence with the calyx tube; petals bright yellow, aging red, narrowly obovate to obcordate, rounded, notched or apiculate, 2.5–3.5 mm. long, 1.5–3.5 mm. wide; longer stamens twice the shorter, glabrous, one-third to one-half length of petals; anthers rounded, 0.5–0.7 mm. long, erect; style equaling longer stamens, glabrous, 2–4.5 mm. long; stigma 0.6–1.0 mm. broad; capsules linear, cylindrical, often torulose, sessile or stalked, truncate or beaked, glandular or pubescent, straight or curved, 15–40 mm. long, 1 mm. or less thick; seeds brown, obovoid, 0.6–1.0 mm. long, minutely cellular-pitted.

The plants that I am including under this species offer an exceedingly puzzling and difficult taxonomy; they are found over practically all western North America, from British Columbia to Lower California and from the Rocky Mountains to the Pacific Ocean. What is apparently the same species occurs in the southern part of South America, but so far as I can ascertain, the name *contorta* has priority over all others. For the most part the species seems to be one that grows in sandy situations along the coast, rivers, sand banks, and the like. In North America I am proposing the recognition of five varieties, although by using very minute and inconstant characters, the number could be doubled.

KEY TO VARIETIES

Plants low, commonly less than 15 cm. tall, with very slender glabrate or finely pubescent leaves less than 2 mm. wide

Capsules sessile, 25–35 mm. long and ending in well-defined beak; E. Washington to W. Nevada and central E. California....9a. *O. contorta* var. *typica*

Capsules distinctly pediceled, not beaked, 17–25 mm. long; E. Washington to Wyoming and the Mohave Desert of California

9b. *O. contorta* var. *flexuosa*

Plants taller or heavier, glabrous or pubescent

Stems densely pubescent with short appressed or incurved hairs; capsules 15–25 mm. long, not beaked; coastal Central California from Sonoma to Monterey counties.....9c. *O. contorta* var. *strigulosa*

Stems glabrous or with spreading pubescence; capsules usually over 25 mm. long

Plants spreading, coarse, grayish, with abundant spreading hair; leaves over 2 mm. wide; capsules sessile or nearly so, not beaked; W. Nevada and adjacent California.....9d. *O. contorta* var. *pubens*

Plants tall, erect, glabrous or some with spreading hair; capsule commonly beaked; leaves usually 1–2 mm. wide; from S. W. Oregon to Lower California, largely in interior valleys of the coastal drainage

9e. *O. contorta* var. *epilobioides*

9A. OENOTHERA CONTORTA Dougl. var. **typica,** n. nom.—*O. contorta* Dougl. ex Hook., l. c.; T. & G., Fl. N. Am. **1**:510. 1840; *Sphaerostigma contortum* Walp. Rep. **2**:78. 1843; Small, Bull. Torr. Bot. Club **23**:189. 1896, in part; Nelson, BOT. GAZ. **40**:58. 1905, in part.

Stems slender, glabrate to finely pubescent, usually 5–10, occasionally 25 cm. tall, spreading; leaves narrow, less than 2 mm. wide; capsules sessile, curved or straight, 25–35 mm. long, ending in a definite beak.

Type locality, "on sandy barren soils of the interior parts of the Columbia River," *D. Douglas*, from photograph of type at Kew (P); ranging east of the Cascade and Sierra Nevada Mountains from Washington to Western Nevada and Eastern Central California: CANADA, Cedar Hill, British Columbia, *Pineo* in 1896 (C): WASHINGTON, Rockland, *Suksdorf* 5098 (S, WS), 5099 (S, WS), 5101 (S, WS), 5100 (S, WS), Pasco, *Piper* 2965b (WS); Bingen, *Suksdorf* 2311 (C, G); Illia, *Lake* & *Hull* in 1892 (WS): OREGON, Hay Creek, *Leiberg* 204 (C, G), in 1894 (WS); the Dalles, *Sheldon* 10277 (G, P, S, WS), 10263 (G, P, S, WS), *Heller* 10091 (G, S), 9262 (S), *Sackley* (G), *Lyall* in 1860 (G); Umatilla, *Jones* in 1902 (P): IDAHO, Burnt River Canyon, *Cleburne* in 1883 (P); Big Willow, Canyon Co., *Macbride* 158 (G, W, WS), 158a (G, W); Weiser, *Jones* in 1899 (P), in 1900 (P); Boise, *Clark* 38 (C, G, P, S, W); New Plymouth, *Nelson* & *Macbride* 777 (W): NEVADA, Tonopah, *Shockley* 147 (P, S); Carson City, *Jones* in 1897 (P), *Anderson* in 1864 (US); Steamboat Springs, *Sonne* in 1887 (C); Empire City, *Jones* in 1882 (P): CALIFORNIA: Chat, *Jones* in 1897; Big Valley, Modoc Co., *Baker* & *Nutting* in 1894 (P).

This variety is much like var. *pubens*, but smaller and more delicate. It has at least four forms: (1) glandular in the inflorescence, *Sonne* at Steamboat Springs, *Heller* 10091, *Sheldon* 10263, and *Jones* at Umatilla and Carson City; (2) glabrous, *Suksdorf* 5098; (3) not glandular, with spreading pubescence, *Suksdorf* 5101, 5099, 5100, *Sheldon* 10277; and (4) not glandular and with appressed pubescence, *Suksdorf* 2311, Clark 38, *Macbride* 158. The low habit, however, and the slender, beaked, sessile capsules are quite constant.

9B. OENOTHERA CONTORTA var. **flexuosa** (Nelson), n. comb.—*Sphaerostigma contortum* var. *flexuosum* Nelson, BOT. GAZ. **40**:58. 1905; *S. flexuosum* (Nelson) Rydb., Fl. Rocky Mts., 601. 1907; *Oenothera parvula* Nutt. in T. & G., Fl. N. Am. **1**:511. 1840; *Sphaerostigma parvulum* Walp., Rep. **2**:78. 1843; *S. filiforme* Nelson, BOT. GAZ. **40**:57. 1905.

Stems and leaves as in var. *typica;* capsules slender, not over

0.5 mm. thick, distinctly pediceled, not attenuate into a beak, 17–25 (–30) mm. long, frequently curved into a half circle.

Type locality, Point of Rocks, Wyoming; ranging with the last but east to Wyoming and south to the Mohave Desert of California: WYOMING: Granger, *Nelson* 4698 (W); Pacific Creek, *Merrill* & *Wilcox* 602 (G, US, W); Point of Rocks, *Nelson* 4760, type coll. (G, W); Ft. Steele, *Tweedy* 4432 (US): UTAH, Deep Creek, *Jones* in 1891 (C, G, P), New River, in 1859, type of *S. filiforme* (M); Gold Hill, *Jones* in 1891 (P, W); Silver Reef, *Jones* 5149n (P); Sevier Bridge, *Jones* in 1880 (P); Thompsons Spring, *Jones* in 1891 (P); Detroit, *Jones* in 1891 (P): NEVADA, Steamboat Springs, *Stokes* in 1903 (C); Truckee Pass, *Kennedy* 1306 (C, NY, S, W); Cobre, *Jones* in 1906 (P), in 1907 (P); Candelaria, *Shockley* 247 (S): CALIFORNIA, Cactus Flat, San Bernardino Mts., *Jones* in 1926 (P), *Munz* 10519 (P); Kramer, *K. Brandegee* in 1913 (C); Argus Mts., *Hall* & *Chandler* 7089 (C); Bishop, *Heller* 8288 (C, G, S), *Jones* in 1927 (P), *K. Brandegee* in 1913 (C); Bishop Creek, *Hall* & *Chandler* 7244 (C, P); Coso Mts., *Coville* & *Funston* 938 (S); Lone Pine, *Jones* in 1927 (P), in 1897 (P, US); Lone Pine Creek, *Hall* & *Chandler* 7208 (C); Chat, *Davy* in 1897 (C); Amedee, *Jones* in 1897 (P): OREGON, Summer Lake, *Eggleston* 6861 (US); Blue Mts., *Cusick* in 1897 (G); Mathew Valley, *Leiberg* 2221 (C, G, P): IDAHO (?), Rocky Mts., "toward Lewis' River," *Nuttall*, type coll. of *O. parvula* (NY): WASHINGTON, Cascade Mts., *Vasey* in 1889 (G, WS); Jct. Crab & Wilson Creeks, *Sandberg* & *Leiberg* 263 (C, G, WS); Pasco, *Piper* 2965a (WS); N. Yakima, *Henderson* in 1892 (WS).

This variety is another variable group. The inflorescence may be (1) glandular, as in *Piper* 2965a, *Sandberg* & *Leiberg* 263, *Hall* & *Chandler* 7244, *Kennedy* 1306; or (2) strigillose, as in *Heller* 8288 and *K. Brandegee* near Bishop; or (3) glandular and strigillose, as in *Henderson* at North Yakima; or (4) glandular and with spreading pubescence, as in *Jones* at Cobre, Nevada. Then too, the capsules may be excessively long, as in the *Vasey* collection in the Cascades, which has them 4 cm. long. *Hall* & *Chandler* 7089, *Jones* from Lone Pine, and others suggest var. *pubens* by their pubescence; in fact many of the plants I refer here have formerly been called *pubens*, but it seems best to restrict that variety to plants of heavier stature and broader leaves.

9c. OENOTHERA CONTORTA var. PUBENS (S. Wats.) Coville, Contr. U.S. Nat. Herb. **4**:104. 1893.—*O. strigulosa* var. *pubens* S. Wats., Proc. Am. Acad. **8**:594. 1873; *Sphaerostigma contortum* var. *pubens* (S. Wats.) Small, Bull. Torr. Bot. Club **23**:189. 1896, in part; Nelson, BOT. GAZ. **40**:58. 1905; *S. pubens* (S. Wats.) Rydb., Bull. Torr. Bot. Club **33**:146. 1906; *S. orthocarpum* Nelson & Kennedy, Proc. Biol. Soc. Wash. **19**:155. 1906.

Coarse-stemmed plants with abundant spreading pubescence;

leaves rather broad, commonly over 2 mm. wide; capsules 1 mm. or more in diameter, 25–35 mm. long, sessile or subsessile, not beaked.

Type locality, Carson City, Nevada, if we select as the type *Watson* 423 (G). In his description, Watson cites first *Fremont* 219 from California in a list of several numbers; but on reference to Bot. King, 112. 1871, where Watson uses "*O. dentata* var." and which describes what he two years later called *pubens*, his own collection is seen to be nearest the true type. The *Fremont* collection probably belongs to var. *epilobioides*. As here restricted, var. *pubens* is found in western Nevada and adjacent California, as follows: NEVADA, Thomas Canyon, *Kennedy* 1872 (US); Empire City, *Jones* 3870 (W); Carson City, *Watson* 423 (G, US), *Anderson* 99 (G), 155 (G), in 1864 (US), *Baker* 971 (C, G, P, US, W); Currant *Bentley* in 1916 (S); Lake View, *K. Brandegee* in 1913 (C); Verdi, *Sonne* in 1888 (C); Reno, *Jones* in 1903 (P), *Diehl* in 1902 (P), *Hillman* in 1893 (P); Pyramid Lake, *Kennedy* 1015a, type of *S. orthocarpum* (W), 1211 (C, US); Hawthorne, *Jones* in 1882 (P); Virginia City, *Jones* in 1882 (P): CALIFORNIA, Sierra Nevada Mts., *Lemmon* in 1875 (US); Doyle Station, *Eggleston* 6741 (US), 6732 (US); Honey Lake, *Brandegee* in 1892 (C); Erskin Creek, *Purpus* 5365 (C, G).

9D. OENOTHERA CONTORTA var. **strigulosa** (F. & M.), n. comb.—*Sphaerostigma strigulosum* F. & M., Ind. Sem. Hort. Petrop. **2**:50. 1835; *Oenothera strigulosa* T. & G., Fl. N. Am. **1**:512. 1840, in part.

Stems densely pubescent, with short appressed or incurved hairs, and growing to be 15–30 cm. tall; capsules short, 15–25 mm. long, not beaked.

Type locality, "Nova California;" ranging along the coast from Humboldt to Monterey counties: CALIFORNIA, *Horto Berol.*, in 1839 (G); *Horto Cantab.*, Anno 1843, e sem. Petrop. (G); Buckport, Humboldt Co., *Tracy* 2191 (C, G); Bodega Bay, *Heller & Brown* 5613 (G, P, S, W); Presidio, *M. S. Baker* in 1904 (P), *C. F. Baker* 711 (P); Golden Gate Park, *Davy* 185 (C); San Francisco, *Rattan* in 1878 (S), *Davy* in 1895 (C), *Greene* in 1893 (C); Lake Merced, *Dudley* in 1901 (S), *Davy* in 1896 (C), *Hall* 1788 (C), *Tracy* 1828 (P, W); Alameda, *Bioletti* in 1891 (C); Colma, *K. Brandegee* in 1905 (C); Antioch, *Rattan* in 1879 (S); Alhambra Valley, *Rattan* in 1887 (S); Holladay Hill, *Rattan* in 1887 (S); Watsonville, *Baker* 1951 (C, G, P, W); Bonnie Doon, Santa Cruz Co., *Dudley* in 1899 (S); San Lorenzo Road, *Dudley* in 1893 (S); Lone Mt., *Rattan* in 1877 (S); San Simeon, *Brandegee* in 1888 (C); Mt. Hamilton, *Elmer* 4625 (C, P, S, US); Bald Peak, *Dudley* 4200 (S); Pacific Grove, *Patterson & Wiltz* in 1907 (S); Carmel Valley, *Randall* in 1910 (S); Monterey, *Dudley* in 1894 (S), in 1901 (S); Del Monte, *Mason* in 1921 (S); Tassajara Road, *Abrams* 5646 (S); San Juan, *Brewer* 715 (C); Pismo Beach, *Abrams* 6513 (S); Santa Rosa Island, *Brandegee* in 1888 (C).

This is a fairly distinct variety with its appressed pubescence and coastal range, but does intergrade to some extent with var. *epilobioides; Elmer* 4625 is quite intermediate in pubescence.

9E. OENOTHERA CONTORTA var. **epilobioides** (Greene), n. comb.—*O. strigulosa* var. *epilobioides* Greene, Fl. Francisc., 216. 1891; *Sphaerostigma contortum* var. *Greenei* Small, Bull. Torr. Bot. Club **23**:189. 1896; Nelson, BOT. GAZ. **40**:58. 1905; *O. dentata* var. *cruciata* S. Wats., Proc. Am. Acad. **8**:594. 1873, in part; *O. strigulosa* var. *cruciata* (S. Wats.) Greene, Fl. Francisc., 216. 1891, in part; *Sphaerostigma campestre* var. *minus* Small, Bull. Torr. Bot. Club **23**:189. 1896, in part; Nelson, BOT. GAZ. **40**:57. 1905, in part.

Large, commonly 2.5–4 dm. high, erect; stems mostly glabrate, but if pubescent, the hair is spreading (especially in plants from Central California); inflorescence often glandular; capsules long, 25–40 mm., sessile, slender, commonly beaked.

Type locality not stated; ranging from Southern Oregon to Northern Lower California in the interior valleys of the region west of the Sierra Nevada and reaching the coast in Southern California: OREGON, Grants Pass, *Henderson* in 1886 (S); Roseburg, *Howell* in 1887 (C, WS); Rogue River, *Leiberg* 4172 (US); CALIFORNIA, Redding, *Heller* 7888 (G); Burney, *Eastwood* 1046 (US); Yosemite, *Abrams* 4426 (G); Tracy, *Baker* 2775 (G); California, *Hartweg* 1733 (G); Poso Creek, *Hall & Babcock* 5012 (G); Santa Cruz, *Anderson* in 1864 (G); Tassajara, *Elmer* 3187 (S); Orcutt, *Jones* in 1926 (P); Santa Barbara, *Elmer* 4001 (G); Carpenteria, *Brewer* 276 (C, G); Topatopa Mts., *Abrams & McGregor* 155 (G); Inglewood, *Abrams* 3237 (G); Elizabeth Lake, *Hall* 3051 (C, G, P, S, W); Cajon Pass, *Parish* 4845 (C, S); San Bernardino Valley, *Parish* 5600 (W), 6935 (C); Moreno Valley, *Hall* 3842 (C); Riverside, *Hall* 2954 (C); Banning, *Jones* in 1903 (P); Kenworthy, *Munz & Johnston* 5466 (C, P); Idyllwild, *Spencer* 2201 (P); Hemet, *Baker* 4116 (C, G, P); Fallbrook, *Jones* in 1882 (P, W); Pala, *Munz* 10371 (P); Oak Grove, *Munz* 10381 (P); Warners Ranch, *Keck & McCully* 53 (P); Cuyamaca Mts., *Munz* 9792 (P); Palomar Mts., *Chandler* 5379 (C); Laguna Mts., *Munz* 9674 (P); Descanso, *Munz & Harwood* 7137 (C, P); Jacumba, *Munz* 8091 (P); Ramona, *Brandegee* in 1894 (C); Foster, *Spencer* 110 (G); Old Mission Dam, *Chandler* 5000 (C): LOWER CALIFORNIA, Hot Springs (Tia Juana), *Jones* in 1882 (C); 50 miles S. E. of Tecate, *Munz* 9548 (P); 9 miles from Tecate, *Munz* 9477 (P).

The name *epilobioides* is used for this variety since it seems to be the oldest one about which there is no uncertainty. The name *cruciata* is older, but seems applicable rather to a group of plants that are intermediate between *O. contorta* var. *epilobioides* and *O. dentata* var. *campestris*, than to *epilobioides* itself. If we apply the principle of selecting as type the first specimen cited in a description,

we should have to choose *Hartweg* 1733 which I refer to var. *epilobioides*, but this does not agree with my interpretation of what WATSON really meant by his *cruciata*. The *Hartweg* collection has petals less than 4 mm. long, while the description gives 4 mm. as the length and agrees with such plants as Oroville, *Heller* 11330 (C, G, S) and Antioch, *Rattan* in 1879 (S), which are small-flowered forms of *dentata*. The name *epilobioides*, as used in this paper, is rather inclusive and has a number of variations, such as (1) inflorescence glandular, *Munz* & *Harwood* 7137, *Chandler* 5379, *Munz* 9548, 10381; (2) inflorescence both glandular and with spreading hair, *Munz* 9477; (3) strigillose, *Munz* 10371, *Baker* 4116; (4) glandular and strigillose, *Munz* 9674, *Munz* 9792; and (5) spreading hairs only, *Munz* 8091. *Hall* 3051 and *Parish* 4845 both are from the edge of the desert region, are low, and resemble var. *typica*.

10. OENOTHERA DENTATA Cav., Ic. 4:67. pl. 398. 1795.—Annual, usually bushy, being freely branched from base; stems subdecumbent to ascending, occasionally subsimple and erect, slender, even capillary, 5–20 cm. high, with light-colored epidermis tending to exfoliate when old, hirsutulose to glabrate, or strigillose or glandular; leaves well distributed, mostly lance-linear, subsessile, often fascicled, pubescent to glabrous, remotely denticulate, acute, 5–30 (–50) mm. long, 1–4 (–7) mm. wide, gradually smaller as one passes up the stem, those of inflorescence reduced to leafy bracts; flowers few, in uppermost axils, not crowded; calyx tube obconic, glabrous within, glandular to strigillose without, 2–4 mm. long; calyx lobes lance-ovate, glandular or strigillose, 3–12 mm. long; petals bright yellow with or without red dots at base, suborbicular-obovate to -obcordate, 5–15 mm. long; filaments glabrous, yellow, distinctly of two lengths, the longer half to two-thirds the length of the petals; anthers oblong, glabrous, 1–2 mm. long, yellow; style glabrous, 6–15 mm. long, usually distinctly shorter than the petals; stigma 0.7–3 mm. broad; capsules linear, terete, somewhat torulose, straight or somewhat contorted, strigillose or glabrate, 2–4 cm. long, 0.5–1.0 mm. thick, with or without terminal beak; seeds brown, linear-obovoid, somewhat angled and flattened, minutely cellular-punctate, 0.5–1 mm. long.

The type of *O. dentata* came from "prope Coquimbo et Talcaguano, urbes Chilenses." The original description and the plate agree fairly well with North American material except for the stigma, which is said to be "quadrifidum." I have not had access to enough South American material to present any treatment including it, and must confine my attention here to that from North America.

KEY TO VARIETIES

Petals 5–8 mm. long; capsules slender, about 0.5 mm. thick; seeds 0.5 mm. long
Stems short-villous in lower portion at least; inflorescence glandular; capsules with well defined beak; in California north of Santa Barbara County and Tehachapi ..... 10a. *O. dentata* var. *campestris*
Stems glabrate or with short appressed hair; inflorescence canescent-strigillose or glandular; capsules not distinctly beaked; Santa Barbara and Tehachapi to Elsinore and Hemet, California ..... 10b. *O. dentata* var. *parishii*
Petals 8–15 mm. long; capsules thicker, about 1 mm. in diameter; seeds about 1 mm. long; Western Mohave Desert into Nevada
10c. *O. dentata* var. *johnstonii*

10A. OENOTHERA DENTATA var. CAMPESTRIS (Greene) Jepson, Man. Calif., 685. 1925.—*O. campestris* Greene, Fl. Francisc., 216. 1891; *Sphaerostigma campestre* (Greene) Small, Bull. Torr. Bot. Club **23**:189. 1896, in part; Nelson, BOT. GAZ. **40**:57. 1905; apparently *O. torulosa* f. *mixta* Leveille and f. *permixta* Leveille, Monogr. Onoth., 180. 1905; and *Sphaerostigma campestre* var. *mixtum* (Levl.) Nelson, l. c.

Stems short-villous below with spreading hair; inflorescence glandular; petals 5–8 mm. long; capsules slender, 0.5 mm. thick, usually with well defined terminal beak; seeds 0.5 mm. long.

Type locality not given, but the description refers back to the *O. dentata* of Watson in Bot. Calif. 1:226. 1876, which is based on that of T. & G. Fl. N. Am. 1:510. Their plant was one collected in California by *Douglas* (G), and which must have come from near the coast. It agrees in pubescence and other characters with what I am including under var. *campestris*. The variety ranges in the San Joaquin and Sacramento valleys and sparingly from Antioch to Santa Barbara: CALIFORNIA, Lakeport, *Baker* in 1903 (C, P); Antioch, *Baker* 2807 (C, G, P, W); Modesto, *K. Brandegee* in 1917 (P); Clovis, *Thompson* in 1902 (P, S); Alcalde, *T. S. Brandegee* in 1891 (C); Lindsay, *Munz* 9084 (P); Greenhorn Range, *Hall & Babcock* 5037 (C, S); Poso Creek, *Dudley* 561 (S); Merced River, *Bolander* 4844 (G); San Antonio Creek, *Dudley* in 1895 (S); Nascimiento River, *State Survey* 550 (C); Santa Margarita fossil bed, *Summers* in 1886 (C, P, W). *Baker* 2807 has rather small flowers (petals 5–6 mm. long) and would be near Watson's var. *cruciata* which was discussed under the preceding species. The *Brandegee* collection from Alcalde and the *Thompson* one from Clovis approach var. *johnstonii* in the large flowers, but not in the pubescence of the stems.

One name that needs discussion is *Sphaerostigma campestre* var. *helianthemiflorum* (Levl.) Nelson, BOT. GAZ. **40**:57. 1905. NELSON does not define his use of the variety, but one would infer that he refers to the large-flowered material that I am calling *johnstonii*. His discussion refers back simply to LEVEILLE'S

description and plate (Monogr. Onoth., 178 and plate. 1905). The plate figures three collections, one of which, *S. B.* and *W. F. Parish* 1304, is var. *parishii;* the second, *Palmer* 136, I have not seen, but it may be var. *johnstonii*; the third is uncertain, but certainly not var. *johnstonii*. Furthermore, LEVEILLE's citation of specimens for his *O. torulosa* race *helianthemiflora* includes plants of var. *campestris* as well. So far as I can see, LEVEILLE meant this race to consist of all the large-flowered material that I refer to *dentata*, while *torulosa* itself was largely what I am calling *contorta*. The name *helianthemiflora*, then, is not based on any particular type or definite or restricted concept, and I feel under no obligation to use it for the large-flowered plants for which I here propose the name:

10B. OENOTHERA DENTATA var. **johnstonii**, n. var.—Stems glabrate or glandular-pubescent; inflorescence glandular-pubescent; leaves up to 6 mm. wide; flower large, petals 10–15 mm. long; calyx lobes 5–12 mm. long; capsules 1 mm. thick, not conspicuously beaked; seeds about 1 mm. long. (Flores magni; lobis calycis 5–12 mm. longis; petalis 10–15 mm. longis; capsulis 1 mm. crassis; seminibus circa 1 mm. longis.)

Type, near Mohave, *I. M. Johnston* on May 5, 1920 (Pomona College Herb. no. 8844); ranging over western half of Mohave Desert and north-eastward into Nevada: NEVADA, Nipton, *Jones* in 1907 (P): CALIFORNIA, Mill Creek Canyon, Panamints, *Coville* & *Funston* 759 (G, S); Shepherds Canyon, *Jones* in 1897 (P); Inyokern, *Bailey* in 1922 (P); Darwin, *Austin* 539 (C); Cameron, *K. Brandegee* in 1884 (C); Hinkley, *Jaeger* 125 (P); Barstow, *Munz* & *Keck* 7931 (P); Garlic Springs, *Munz* & *Keck* 7869 (P); Granite Wells, *Parish* 10117 (S); Randsburg-Rand, *K. Brandegee* in 1913, in part (C); Rosedale, *Abrams* in 1900 (S); Sunset, *Heller* 7728 (C, G, S); Devils Den, *Pierce* in 1922 (P); Tehachapi, *Brandegee* in 1884 (C), *Jones* in 1903 (P), *Munz* 8961 (P); Gormans Station, *Parish* 1973 (G, S); N. of Tejon Pass, *Munz* 9003 (P); Mohave, *Heller* 7762 (C, G, S); Tejon Pass, *Dudley* & *Lamb* 4442 (P, S); Willow Springs, *Munz* 10043 (P); Grapevine, *Newsom* & *Hilend* in 1927 (P); Elizabeth Lake, *Hall* 3066 (C), *Munz* 9989 (P); Oil City, *Heller* 7590 (C, G, S).

10C. OENOTHERA DENTATA var. **parishii** (Abrams), n. comb.—*Sphaerostigma campestre* var. *parishii* Abrams, Fl. Los Angeles, 272. 1904; *S. campestre* of Small, Bull. Torr. Bot. Club **23**:189. 1896, in part.

Stems glabrate or with short appressed hair; inflorescence usually canescent, sometimes glandular; flowers as in var. *campestris;* capsules slender, 0.5 mm. thick, not distinctly beaked; seeds 0.5 mm. long.

Type locality near San Bernardino; range over western half of Mohave Desert and occasional in interior valleys from Santa Barbara to Los Angeles counties, more common from San Bernardino to Elsinore and Hemet: CALIFORNIA, Terra Bella, Tulare Co., *Abrams* 10855 (S); Caliente Creek, *Munz* 8989 (P); Mt. Pinos, *Hall* 6439 (C); Ft. Tejon, *Hall* 6276 (C); Mohave, *Jones* in 1903 (P); Lebec, *Jones* in 1927 (P); Pallett Creek, *Munz* 6904 (P); Acton, *Elmer* 3715 (G, P, S); Swartout Canyon, *Hall* in 1899 (C); Victorville, *Munz* 2557 (P, S); Barstow, *Hall* & *Chandler* 6849 (C, P); Daggett, *Hall* 6141 (C); Argus Mts. *Purpus* 5436 (G); Leastalk, *Parish* 10361 (S); Cajon Pass, *Munz* 4475 (P); San Bernardino Valley, *Parish* 7102 (C), in 1893 (C), in 1901 (S); Riverside, *Koethen* 16 (C); Hemet, *Baker* 4115 (C, P, S); Winchester, *Hall* 2417 (C, P, S, W); San Jacinto, *Jones* 3168 (C, P, W); Elsinore, *McClatchie* in 1892 (S).

Most of the material referred here is not glandular, but the following collections are: *Munz* 4475, *Hall* 6439, 6276, *Munz* 6904, *Elmer* 3715, and *Hall* & *Chandler* 6849.

11. OENOTHERA GUADALUPENSIS S. Wats., Proc. Am. Acad. **11**:115. 1876.—Annual, erect, 8–10 cm. high, simple or branched from base, strigillose pubescent throughout; stems leafy; leaves oblanceolate, "sessile or the lowest attenuate into a petiole, obtuse or acutish, obscurely sinuate-toothed," 2–3 cm. long, about 1 cm. wide; "flowers few, axillary"; calyx tube obconic, 2.5 mm. long, glabrous within; calyx lobes ovate, 2.5 mm. long; petals narrowly obovate, yellow, 2.5–3 mm. long; filaments glabrous, 1 to 2 mm. long; anthers rounded, scarcely 1 mm. long; style glabrous, 3.5 mm. long; stigma about 1 mm. broad; capsules strigose "oblong-pyramidal," nearly straight, strongly angled, about 12 mm. long, 2.5 mm. in diameter; seeds "brown, smooth."

Collected on Guadalupe Island by *E. Palmer* in 1875 (G); this, the type collection, is all that I have seen. It offers scarcely enough material to satisfy me as to whether *O. guadalupensis* is specifically distinct or whether it should be reduced to varietal rank under *O. hirta* Link.

12. OENOTHERA HIRTA Link, Enum. Hort. Berol. **1**:378. 1821.—*Sphaerostigma hirtum* F. & M., Ind. Sem. hort. Petr. **2**:22. 1835; *Oenothera micrantha* Hornem., ex Sprengel, Syst. **2**:228. 1825; not *O. hirta* L., Syst. Ed. X, 998. 1760.

Annual, simple or several-stemmed, prostrate to ascending or erect, glabrate to hirsute, 5–60 cm. tall, leafy throughout, with stems pale to reddish, and with readily exfoliating epidermis; basal leaves forming a sort of rosette, linear-lanceolate to oblanceolate, pubescent

to pilose, almost entire, obtuse to acute, 20–100 mm. long, 4–15 mm. wide, gradually narrowed into equal or shorter petioles; lower cauline leaves shorter and broader, subsessile to short-petioled; upper cauline leaves sessile, lance-linear to lance-oblong to ovate-clasping, largely secund and often undulate, gradually reduced up the stem; flowers in axils of even lowest leaves; calyx tube 1.5–5 mm. long, glabrate to pubescent within, glabrate to pilose without; calyx lobes lanceolate, 1–7 mm. long, glabrate to pilose; petals yellow often drying green, 1.5–7 mm. long, obovate to obcordate, emarginate, rounded or salient-toothed; stamens of two lengths, the longer ones about two-thirds length of petals, shorter ones about half the length; anthers oblong to linear-oblong, 0.5–1.0 mm. long; style equaling longer stamens, glabrate; stigma 0.5–1 mm. broad; capsules curved or contorted, quadrangular, glabrous to pubescent, 1–2 mm. thick, 10–25 mm. long, gradually attenuate upward and usually beaked; seeds brown, obovoid, finely cellular-pitted, ca. 1 mm. long.

KEY TO VARIETIES

Flowers small, petals 2–3 (-4) mm. long; stems and leaves hirsutulous or villous, but not pallid

Stems semi-prostrate; cauline leaves oblong-lanceolate, obtuse, sessile but not clasping; largely coastal ..... 12a. *O. hirta* var. *typica*

Stems erect or ascending; cauline leaves oblong-ovate to broadly ovate, acute, with subcordate clasping base; largely of the interior valleys 12b. *O. hirta* var. *jonesii*

Flowers larger; petals 3–7 mm. long; foliage either glabrate, or pallid with close whitish pubescence

Plants glabrate; stems often simple, erect; interior valleys of costal drainage 12c. *O. hirta* var. *ignota*

Plants pallid with whitish pubescence; stems mostly several from near the base, spreading; deserts ..... 12d. *O. hirta* var. *exfoliata*

12A. OENOTHERA HIRTA Link var. **typica,** n. nom.—*O. hirta* Link, l. c., *Sphaerostigma hirtum* F. & M., l. c.; *Oenothera micrantha* Hornem., in Sem. hort. bot. hafn., 16. 1822, without description; ex Sprengel, Syst. **2**:228. 1825; *Holostigma micranthum* Spach, Nouv. Ann. Mus. Par. **4**:335. 1835; *Sphaerostigma micranthum* Walp., Rep. **2**:77. 1843; *O. cheiranthifolia* var. *contorta* of Levl., Mon. Onoth., 216. 1905, in large part.

Semi-prostrate; basal leaves oblanceolate; cauline leaves oblong-

lanceolate, sessile, obtuse, undulate, denticulate, commonly 5–7 mm. wide; flowers small; petals 2–4 mm. long; capsules short, 12–20 mm. long.

Type locality, California, probably from the northern coast; ranging largely along the coast from Bodega Point to Lower California: CALIFORNIA, Antioch, *Baker* 2808 (C, G, P, W); San Francisco, *Curran* in 1894 (S), *Davy* in 1896 (C); Mt. Diablo, *Abrams* 8022 (S); Del Monte, *Heller* 6659 (C, G, P, S); San Antonio Mission, *Dudley* in 1895 (S); Paso Robles, *Barber* in 1899 (C); Pismo Beach, *Abrams* 6513 (S); Santa Rosa Island, *Brandegee* in 1888 (C); Buellton, *Munz* 10289 (P); Santa Susanna Mts., *Brewer* 221 (C); Santa Monica Mts., *Crawford & Hiatt* in 1916 (P, S); Inglewood, *Abrams* 3232 (C, G, P, S); Ballona Harbor, *Abrams* 1192 (P, S); Claremont, *Robinson* 93 (P); Temescal Mts., *Brewer* 155 (C); Fallbrook, *Jones* in 1882 (P, C, W); San Diego, *Jones* in 1882 (P); Bird Rock, *F. E. & E. S. Clements* 184 (C, G), 185 (C, G); Jamul, *Stokes* in 1895 (S): LOWER CALIFORNIA, San Pedro Martir, *Brandegee* in 1889 (C); San Telmo, *Brandegee* in 1893 (C); San Quentin Bay, *Palmer* 617 (C, US), 656 (US); San Antonio Canyon, *Ballou* 108 (P).

The varieties in this species are not any too well marked and intergradation is frequent. The leaf shape and habit of this variety and of var. *jonesii* are so variable as to make many plants difficult of determination; the following may be cited as intergrades: Mt. Hamilton-Livermore Road, *Bacigalupi* in 1923 (S); Mill Valley, *Bioletti* in 1892 (W); Santa Barbara, *Brewer* 324 (C); Bardsdale, Ventura Co., Hall 3241 (C); Santa Monica Mts., *Abrams* 1273 (S).

I have a photograph of the type of *O. micrantha* Hornem. and have had access to authentic material of *O. hirta* Link (NY). CHRISTENSEN of Copenhagen has kindly given me information showing the identity of these two species. Since LINK's name is the older, and since LINNAEUS' *O. hirta* is universally regarded as a *Jussiaea*, I here take up the name *hirta* for the plant so long called *micrantha*.

12B. OENOTHERA HIRTA var. JONESII Leveille, Mon. Onoth., 213. 1905.—*Sphaerostigma micranthum* var. *jonesii* (Levl.) Nelson, BOT. GAZ **40**:59. 1905; *Oenothera hirtella* Greene, Fl. Francisc., 215. 1891.; *Sphaerostigma hirtellum* (Greene) Small, Bull. Torr. Bot. Club **23**:190. 1896; Nelson, BOT. GAZ. **40**:59. 1905; *S. arenicolum* Nelson, BOT. GAZ. **40**:58. 1905.

Erect or ascending, densely villous-pubescent throughout; cauline leaves oblong-ovate to broadly ovate, acute, often sessile, with subcordate clasping base; flowers as in *typica*.

Type not stated, but description refers to plate showing *Jones* 2231 from Santa Cruz, California, which I take to be the type and not *Hansen* 543 as cited by NELSON, although LEVEILLE gives the latter first in the list of collections

belonging here. This variety tends to occur on hills and lower mountains of the interior valleys: CALIFORNIA, Anderson Valley, Mendocino Co., *Purdy* in 1882 (G); Lakeport, *Tracy* 1701 (C); Alder Springs,, Glenn Co., *Heller* 11443 (G, S); Knoxville, Napa Co., *Jepson* in 1892 (C); Mt. Diablo, *Bioletti* in 1894 (C); Santa Cruz, *Jones* 2231, type coll. (P); Loma Prieta, *Hichborn* in 1920 (S); Los Gatos, *Heller* 7337 (C, G, S, W); Pajaro Hills, *Chandler* 436 (C); Monterey, *Elmer* 3192, type coll. *S. arenicolum* (S); Santa Lucia Mts., *Abrams* 7410 (S); Santa Ynez Mts., *Elmer* 3943 (G, P, S); Drytown, Amador Co., *Hansen* 543 (C, P, S); Erskin Creek, *Purpus* 5099 (C); Bouquet Canyon, *Munz* 6928 (P); Santa Monica, *Munz* & *Harwood* 3928 (P); San Gabriel Canyon, *Munz* 9427 (P); Claremont, *Chandler* in 1897 (C); Victorville, *Parish* 10624 (S); Strawberry Valley, San Jacinto Mts., *Wilder* 954 (C); Poppet Flat, *Munz* & *Johnston* 8847 (P); Santa Rosa Mts., *Munz* 5940 (P); Santiago Peak, *Munz* 7064 (C, P); Elsinore, *Munz* 5086 (P); Dripping Spring, *Munz* 9833 (P); Henshaw Dam, *Munz* 8333 (P); Santa Ysabel, *Munz* 9809 (P); Campo, *Abrams* 3558 (C, G, P, S); Barrett Dam, *Munz* 8002 (P); Ocean Beach, dist. C. *F. Baker* 1645 (C, G, P, W): LOWER CALIFORNIA, 13 miles S. E. of Tecate, *Munz* 9516 (P); San Quentin, *Brandegee* in 1889 (C); Cardon Grande, *Brandegee* in 1889 (C); Todos Santos, *Orcutt* in 1882 (C); Rosario, *Orcutt* in 1886 (C).

In the mountains of Southern California, occurring in the same fields with the usual form, grows a plant with the petals variously toothed, commonly having a long central tooth with a sinus and shorter tooth on each side. This variation, which is not at all constant, may be designated as *O. hirta* var. *jonesii* forma **reedii** (Parish), n. comb. (*Sphaerostigma bistorta* var. *reedii* Parish, Muhlenbergia 3:60. 1907; *Oenothera micrantha* var. *reedii* Jepson, Man. Calif., 684. 1925; *Sphaerostigma hirtellum* var. *montanum* Davidson, Muhlenbergia 3:108. 1907, in part). Here may be cited PARISH'S type, Waterman Road, San Bernardino Mts., *Parish* 5794 (*C, G*); Poppet Flat, *Munz* & *Johnston* 8846 (P); Oak Grove trail to Palomar Mt., *Munz* 10390 (P).

12c. OENOTHERA HIRTA var. **ignota** (Jepson), n. comb.—*O. micrantha* var. *ignota* Jeps., Man. Calif., 684. 1925.

Glabrate; stems often simple, erect; calyx glabrate; flowers larger; petals 5–7 mm. long.

Type locality, Jurupa Hills, near Riverside, California: CALIFORNIA, Pollasky, Madera Co., *Heller* 8166 (C, G, S); Leonis Valley, *Davy* 2620 (P); Kern River Canyon, *G. D. Abrams* in 1900 (S); Ft. Tejon, *Davy* 2375 (C); Mt. Piños, *Dudley* & *Lamb* 4698 (S); Saugus, *Munz* 10013 (P); Antelope Valley, *Davy* 2529 (P); North Baldy Mt., *Abrams* & *McGregor* 579 (S); Mt. Wilson, *Grant* in 1900

(S); San Gabriel Canyon, *Munz* 9461 (P); San Dimas Canyon, *Munz* & *Harwood* 3692 (P, W); San Bernardino, *Parish* in 1901 (S), 3670 (C, G); Waterman Canyon, *Jones* in 1926 (P); Colton, *Jones* in 1882 (P); Slover Mt., *Parish* 73 (C, G, S); Jurupa Hills, *Wilder* 90, type coll. (C), *Johnston* in 1920 (P); Corona, *Munz* & *Harwood* 3373 (P, S); Elsinore, *McClatchie* 77 (S); San Jacinto Valley, *Reinhardt* in 1897 (C); Potrero Grade, *Munz* 9468 (P); Laguna Mts., *Munz* 9677 (P); Fallbrook, *Jones* in 1882 (C, P, W): LOWER CALIFORNIA, 50 miles S. E. of Tecate, *Munz* 9559 (P).

The var. *ignota* is another variation but a real entity. Intergrades with var. *typica* are as follows: Wilson Trail, *Abrams* 1505 (S); Fallbrook, *Abrams* 3326 (C, P, S); Saugus, *Davy* in 1901 (C); Jamesburg, Monterey Co., *Bacigalupi* 1143 (S). In these plants the flowers are rather large for var. *typica*, having petals 4–5 mm. long; the leaves are lanceolate and somewhat narrow and hairy for var. *ignota*. Another set of intergrades is with var. *jonesii;* they tend to have flowers large for *jonesii*, and leaves wide, and to be rather hairy for var. *ignota:* Oak Grove Trail to Palomar Mt., *Munz* 10398, 10400 (P); Arrowhead Lake, *Hilend* in 1923 (P); Acton, *Barber* 221 (C); Topango, *Munz* & *Harwood* 3968 (P); Jacumba, *McGregor* 112 (S). Another series intergrades with the var. *exfoliata*, tending to have the pallid condition suggesting the latter variety, but the erect habit of growth of *ignota:* Idyllwild Road from Banning, *Munz* 8142 (P); Fullers Mills Mts., *Hall* in 1901 (C); Borrego Spring, *Jones* in 1906 (P); mesas west of Independence, *Hall* & *Chandler* 7300 (C, P, W).

12D. OENOTHERA HIRTA var. **exfoliata** (Nelson), n. comb.—*Sphaerostigma micranthum* var. *exfoliatum* Nelson, BOT. GAZ. **40**:59. 1905; *Oenothera micrantha* var. *abramsi* (Macbr.) Jepson, Man. Calif., 684. 1925; *O. abramsi* Macbr., Contr. Gray Herb. **65**:41. 1922; *Sphaerostigma pallidum* Abrams, Bull. Torr. Bot. Club **32**:539. 1905.

Plant pallid with dense whitish pubescence; stems usually several from near the base, spreading; flowers rather large; petals 3–6 mm. long.

Type locality, Colorado Desert; confined to the deserts and desert borders: CALIFORNIA, Antelope Valley, *Hall* 3052 (C); north side of Cajon Pass, *Munz, Harwood,* & *Johnston* 4075 (P); Cactus Flat, *Munz* 10518 (P); Providence Mts., *Munz, Harwood,* & *Johnston* 4017 (P, W), *Munz* & *Harwood* 3442 (C, P); Quail Springs, *Munz* & *Johnston* 5277 (P); Cabazon, *Munz, Street,* & *Williams* 2360 (P, S); Palm Springs, *Johnston* 1110 (P, S, US), *Spencer* 1452 (P, G); Indian Wells, *Munz* & *Keck* 4978 (P); Coyote Canyon, *Hall* 2791 (C, US); San Felipe Valley, *Keck* & *McCully* 70 (P); Mountain Spring, *Mearns* 3037 (US), *Peirson* 2879 (P); Cholla Ranch, *Jones* in 1906 (P): ARIZONA, Congress, *Orcutt* in 1896 (C); Chloride, *Jones* in 1903 (P); Yucca, *Jones* in 1884 (P); Skull Valley, *Jones* in 1903 (P); Tempe, *Ganong* & *Blaschka* in 1892 (G); Verde River, *Smart* 146 (G).

The species has only one good variety on the deserts, the pallid var. *exfoliata* with its rather large flowers. It and the var. *ignota* stand between *O. hirta* Link and *O. bistorta* Nutt., so far as flower size is concerned. As a varietal name *exfoliata* has priority over any other given to the desert plant. There are two forms: one with narrow almost linear leaves, *Spencer* 1452, *Johnston* 1110, *Munz & Harwood* 3442; and a less common one, with leaves broader and suggesting the var. *jonesii*, *Jones* at Skull Valley and Yucca, and *Munz* 10518.

13. OENOTHERA BISTORTA Nutt., ex T. and G., Fl. N. Am. 1:508. 1840.—Annual, occasionally simple, but usually with several prostrate or ascending stems, these strigose to villous, light in color, often tinged reddish, with exfoliating epidermis, rather slender, 5–80 cm. long; leaves pubescent to thinly pilose, denticulate or subentire; those of the basal rosette 3–7 cm. long, 0.3–0.5 cm. wide, linear-oblanceolate, narrowed into petioles 1–4 cm. long; cauline leaves often secund, shorter and wider than basal ones; uppermost lanceolate to lance-oblong or lance-ovate, acute to obtuse, subsessile to cordate-clasping, 1–3 cm. long, 0.5–2 wide; flowers in axils, only a few in anthesis at once; calyx tube obconic, 3–5 mm. long, glabrate to pubescent within, villous without; calyx lobes villous, lanceolate, 7–10 mm. long; petals yellow, often drying greenish, with or without dark spot at base, suborbicular to obovate to obcordate, 8–14 mm. long; filaments glabrous, distinctly of two lengths, longer ones half to two-thirds the length of the petals; anthers 2.5–3 mm. long, yellow; style glabrate to finely pubescent, 7–11 mm. long, slightly exceeding stamens; stigma 1–1.5 mm. broad; capsule curved or contorted, 1.5–2.5 mm. thick, 12–40 mm. long, with or without beak, pubescent, somewhat quadrangular; seeds brown, obovoid, about 1 mm. long, finely cellular-pitted.

KEY TO VARIETIES

Foliage in general, green; plants of coastal drainage

Capsule short, 12–15 (-20) mm. long, sharply quadrangular, usually 2–2.5 mm. thick, with beak lacking or not exceeding 4–5 mm.; strictly coastal, largely in San Diego region.....13a. *O. bistorta* var. *typica*

Capsule longer, 20–40 mm., more slender, 1.5–2 mm. thick, and with beak 3–10 or more mm. long; rather generally distributed in coastal drainage of Southern California.....13b. *O. bistorta* var. *veitchiana*

Foliage pallid with short appressed hair; desert plants

13c. *O. bistorta* var. *hallii*

13A. OENOTHERA BISTORTA Nutt. var. **typica**, n. nom.—*O. bistorta* Nutt., l. c.; Watson, Proc. Am. Acad. **8**:592. 1873; *Sphaerostigma bistortum* (Nutt.) Walp., Rep. **2**:77. 1843; Small, Bull. Torr. Bot. Club **23**:190. 1896; Nelson, BOT. GAZ. **40**:59. 1905; probably *Holostigma bottae* Spach, Nouv. Ann. Mus. Paris (III) **4**:336. 1835; *Oenothera spiralis* var. *linearis* Jepson, Man. Calif., 684. 1925.

Capsule short, 12–15 (-20) mm. long, sharply quadrangular, usually 2–2.5 mm. thick, with beak lacking or not over 4 or 5 mm. long.

Type locality, San Diego; ranging along the very coast from Ballona Harbor and Catalina Island to San Diego and northern Lower California: CALIFORNIA, Catalina Island, *Trask* in 1896 (C); Ballona Harbor, *Abrams* 300 (P); Canada Salada, *Peirson* 3411 (P); Laguna Beach, *Crawford* in 1916 (P); Sunnyside, *Hall* 3907 (C), 3908, type coll. of *O. spiralis* var. *linearis* (C); La Jolla, *F. P.* & *E. S. Clements* 181 (C, G), 182 (G), *Chandler* 5138 (S); Soledad, *Jones* in 1882 (P); Torrey Pines Park, *Munz* 7956 (P); Del Mar, *Brandegee* in 1894 (C); San Diego, *Nuttall*, type of *O. bistorta* (G), *K. Brandegee* in 1906 (C, P), *Jones* 3058 (P, W), San Diego River near the mission, *Abrams* 3412 (C, G, P, S); Sweetwater Valley, *Stokes* in 1895 (S); Point Loma, *Eastwood* 2864 (G); San Pasqual, *Thurber* 602 (G): LOWER CALIFORNIA, Hot Springs, now Tia Juana, *Jones* in 1882 (C, P, W).

Intergrades between this variety and the var. *veitchiana* are as follows: Ballona, *Abrams* 1232 (P, S) and Playa del Rey, *Grant* in 1904 (W), San Diego, *C. F. Baker* distribution 3395 (C, G, P), all of which have capsules quite intermediate in character.

13B. OENOTHERA BISTORTA var. VEITCHIANA Hook., Bot. Mag. **84**:pl. 5078. 1858.—*O. bistorta* var. *veitchiana* in Watson, Proc. Am. Acad. **8**:593. 1873; *Sphaerostigma veitchianum* (Hook.) Small, Bull. Torr. Bot. Club **23**:191. 1896; *S. bistortum* var. *veitchianum* (Hook.) Nelson, BOT. GAZ. **40**:59. 1905.

Capsule more slender, 1.5–2 mm. thick, and longer, 20–40 mm. with the beak 3–10 or more mm. long.

Type locality, near San Gabriel, Los Angeles County, California; ranging rather generally through the interior valleys and hills of the coastal drainage of Southern California as well as along the coast itself: CALIFORNIA, South Fork of the Kern, *Purpus* 5718 (C): Ft. Tejon, *Xantus* in 1857–8 (G); Springville, *Davy* in 1901 (C); Moorpark, *Abrams* 10129 (P, S); Ojai, *Peckham* in 1866 (US); Santa Clara River, Ventura Co., *Gray* in 1885 (G); Bardsdale, *Hall* 3241c (C), 3241 b (C), 3241*a* (C); Saugus, *K. Brandegee* (C), *Munz* 10018 (P); San Fernando, *Munz* 9383 (P); Pasadena, *Grant* in 1905 (W); Monrovia, *Baker* 4171

(G, P); Claremont, *Munz* 2063 (P); Hesperia, *Shaw*, et al. in 1917 (P); Colton, *Jones* in 1882 (P); San Bernardino, *Parish* 3659 (C, G); Redlands, *Billings* in 1924 (S); Highlands, *Spencer* 1111 (G, P); Hemet, *Baker* 4118 (C, G, P, S); Dripping Springs, *Munz* 9838 (P); Pala, *Munz* 10370 (P); Fallbrook, *Munz* & *Harwood* 3894 (P); San Diego, *K. Brandegee* in 1906 (C); Julian, *Hall* in 1925 (P).

There is considerable intergradation between this plant and the inland forms of the preceding species (*O. hirta* Link). The principal definite character separating them is flower size, and that, especially in depauperate and late season plants, is none too constant. *Munz* & *Harwood* 3894a (P) from Fallbrook, *Hall* 429 from Winchester (C), and *Abrams* 2791 from Fredalba (S) are all examples of plants with small flowers, petals 4–5 mm. long, and except in habit, suggest *O. hirta* var. *ignota*. Usually in pressed specimens the flowers of *O. bistorta* have the petals spread, while in *O. hirta* var. *ignota* they do not.

13c. OENOTHERA BISTORTA var. HALLII (Davidson) Jepson, Man. Calif., 685. 1925.—*Sphaerostigma hallii* Davidson, Muhlenbergia 3:107. 1907.

Foliage pallid with short appressed hair.

Type locality, Banning; CALIFORNIA, Southern California, *Parry* & *Lemmon* 126 (G); Banning, *Hall* 446, type coll. (C), *Munz*, *Street*, & *Williams* 2363 (P, S,), *Jones* in 1903 (P); Indio, *McGregor* 707 (S); Warners Hot Springs, *Eastwood* 2592 (G). This rather uncommon variety corresponds, among the plants belonging to this species, to the var. *exfoliata* for the pallid desert plants of *O. hirta*.

14. OENOTHERA CHEIRANTHIFOLIA Hornem., ex Spreng., Syst. 2:228. 1825.—*Holostigma cheiranthifolium* (Hornem.) Spach, Nouv. Ann. Mus. Paris (III) 4:335. 1835; *Chamissonia cheiranthifolia* (Hornem.) Raim., in Engl. & Prantl, Nat. Pfl. Fam. 3:Abt. 7, 217. 1893.

Annual to perennial, with several prostrate to decumbent wiry or tough stems "radiating from a central rosette crowning the taproot," these 1–6 dm. long; plant rarely glabrous, usually closely white-pubescent to hirsute; leaves thick, those of rosette oblanceolate, 1–7 cm. long, 0.5–1.5 cm. wide, obtuse, subentire to remotely serrulate, narrowed into petioles 1–2 cm. long; lower cauline leaves lance-oblong to oblance-oblong, subsessile to short-petioled, obtuse, subentire to remotely denticulate, 2–4 cm. long, 0.5–1.5 wide; upper cauline leaves sessile, oblong-ovate to orbicular-ovate, obtuse, subentire, 0.5–2.5 cm. long, 0.5–2 cm. wide; flowers single in axils, mostly not near the base of the stems; calyx tube obconic, 2.5–7 mm. long, glabrous or glabrate within; calyx lobes lanceolate, 4–15 mm. long;

petals bright yellow, with or without reddish spots at base, usually drying green, sometimes pinkish, obovate, 7–22 mm. long and equally wide; filaments glabrous, 3.5–6 mm. long or 4.5–8 mm. long; anthers glabrous, linear, 1–2 mm. long; style usually glabrous, 8–22 mm. long; stigma 1–1.5 mm. broad; capsule coiled, distinctly quadrangular, short-beaked or not at all beaked, glabrous or pubescent, 12–22 mm. long; seeds blackish-brown, obovoid, 1 mm. long, minutely cellular-pitted.

KEY TO VARIETIES

Plant pubescent throughout
  Petals 5–9 mm. long; plant grayish pubescent; along coast from Point Conception, California northward.... 14a. *Oenothera cheiranthifolia* var. *typica*
  Petals 10–22 mm. long; plant silvery; Point Conception southward 14b. *O. cheiranthifolia* var. *suffruticosa*
Plant glabrous throughout; rare, San Miguel Island and coast of Monterey County..... 14c. *O. cheiranthifolia* var. *nitida*

14A. OENOTHERA CHEIRANTHIFOLIA Hornem. var. **typica,** n. nom.—*Oenothera cheiranthifolia* Hornem., l. c.; Wats., Proc. Am. Acad. **8**:592. 1873; *O. spiralis* Hook., Fl. Bor. Am. **1**:213. 1833; Leveille, Monogr. Onoth., 220. 1905, in part; *Holostigma spirale* (Hook.) Spach, Nouv. Ann. Mus. Paris (III) **4**:336. 1835; *Sphaerostigma spirale* (Hook.) F. & M., Ind. Sem. Hort. Petrop. **2**:50. 1835; Small, Bull. Torr. Bot. Club **23**:190. 1896; Nelson, BOT. GAZ. **40**:60. 1905; *Holostigma cheiranthifolium* (Hornem.) Spach, l. c.; *Sphaerostigma cheiranthifolium* (Hornem.) F. & M., l. c.; *Chamissonia cheiranthifolia* Raim., in Engl. & Prantl., l. c.; *Agassizia cheiranthifolia* (Hornem.) Spach, Hist. Nat. Veg. Phaner., **4**:348. 1825.

Plants grayish-pubescent throughout; flowers rather small, petals 5–9 mm. long.

Type locality, California, collected by WORMSKIOLD. In the original description, the type locality is given as Chile, a statement that has caused much confusion. At the Botanical Museum at Copenhagen there are three sheets, one with the following in HORNEMANN's handwriting, "Ex hort. semina e California mis. WORMSKIOLD," the second indicating that it came from WORMSKIOLD in 1820, and the third from "hb. Berol." On none of these does the name Chile appear, according to Dr. H. M. HALL of the Carnegie Institution, who kindly examined them for me. In addition to photographs and fragments from CHRISTENSEN of Copenhagen, I have seen a sheet at the Gray Herbarium from "Hort. Hamburg, Wormskiold." *O. cheiranthifolia* is a strand plant. The following

material is representative of the var. *typica*—"N.W. Coast" of America: *Menzies*, type of *O. spiralis*, photo of Kew specimen (P): OREGON, Port Orford, *Peck* 8506 (G); Gold Beach, Curry Co., *Hoyt* 76 (S); Chitco, *Howell* in 1884 (G); Sunset Cove, Coos Co., *Abrams* & *Benson* 10595 (S, W): CALIFORNIA, Eureka Peninsula, *Dudley* in 1899 (S); Clam Beach, *Munz* 9891 (P); Ocean Beach, *Tracy* 1263 (C); Samoa, *Tracy* 3017 (C, G, S); Ft. Bragg, *Duncan* 236 (S, W); Bodega Point, *Eastwood* 4832 (G); Oakland, *Jones* 2371 (P); San Francisco, *Baker* 697 (C, G, P); Del Mar, *Hichborn* 322 (S); Del Monte, *Heller* 6655 (C, G, P, S, W); Morro, *Munz* 9240 (P); Santa Rosa Island, *Brandegee* in 1888 (C); Santa Barbara Island, *Hemphill* (C); Surf, *Elmer* 3909 (G, P, S).

While flower size and, to a less extent, character of pubescence distinguish var. *typica* and var. *suffruticosa*, some plants are quite intermediate and difficult to place definitely. Examples are from Playa del Rey, *Grant* in 1904 (S) with small flowers, and from Santa Barbara, *Brandegee* in 1889 (C).

14B. OENOTHERA CHEIRANTHIFOLIA var. SUFFRUTICOSA S. Wats., Proc. Am. Acad. **8**:592. 1873.—*O. viridescens* Hook., Fl. Bor. Am. **1**:214. 1833; *Sphaerostigma viridescens* (Hook.) Walp., Rep. **2**:77. 1843; Small, Bull. Torr. Bot. Club **23**:190. 1896; *Oenothera spiralis* var. *viridescens* (Hook.) Jeps., Man. Calif., 684. 1925; *Sphaerostigma spirale* var. *viridescens* (Hook.) Nelson, BOT. GAZ. **40**:60. 1905; *S. cheiranthifolium* var. β, F. & M., Ind. Sem. Hort. Petrop. **2**:50. 1835; *S. spirale* var. *clypeatum* (Levl.) Nelson, BOT. GAZ., l. c.; *Oenothera virescens* of Greene, Fl. Francisc., 214. 1891.

Foliage silvery; perennial and usually suffrutescent; flowers large; petals 13–22 mm. long.

Type locality, California (*Coulter* 153, probably from near Santa Barbara or to the south); ranging along the strand from Santa Barbara to northern Lower California: "N. W. America:" *Menzies*, photo of type of *O. viridescens* (P): CALIFORNIA, Santa Barbara, *Elmer* 4018 (G, P, S); Carpinteria, *Hall* 3169 (C); Ventura, *Abrams* 10144 (P, S); Hueneme Beach, *Munz* 9393 (P); Santa Monica, *Barber* 24 (C); Redondo, *Grant* 1238 (W); Playa del Rey, *Grant* E1235 (W); Seal Beach, *Kendall* in 1920 (P); Ballona Harbor, *Abrams* 1679 (P, S); Balboa, *Abrams* 6576 (S); Laguna Beach, *Peirson* 4670 (P); Del Mar, *Brandegee* in 1894 (C); Oceanside, *Abrams* 6588 (S); La Jolla, *F. E.* & *E. S. Clements* 178, 179, 180 (C, G); San Diego, *Nuttall* (G), *Jones* in 1882 (P), *Wright* 52 (C); Coronado, *Chandler* 5090 (S), *Spencer* 112 (G, P): LOWER CALIFORNIA, Tia Juana, *Diehl* 214 (P); Ensenada, *Brandegee* in 1899 (C); San Quentin, *Ballou* & *Canby* in 1925 (P); Socorro, *Brandegee* in 1889 (C).

14C. OENOTHERA CHEIRANTHIFOLIA var. **nitida** (Greene), n. comb.—*O. nitida* Greene, Pittonia **1**:70. 1887; *Sphaerostigma niti-*

dum (Greene) Small, Bull. Torr. Bot. Club **23**:190. 1896; Nelson, BOT. GAZ. **40**:58. 1905; *Oenothera spiralis* var. *nitida* (Greene) Jepson, Man. Calif., 684. 1925.

Flowers like those of var. *typica*, with petals 5–8 mm. long; plants glabrous throughout.

Type locality, San Miguel Island: CALIFORNIA, San Miguel Island, *Greene* in 1886, type coll. (C); between Castroville and Monterey, *K. Brandegee* in 1908 (C, G, W); Monterey County, *K. Brandegee* in 1889 (S); Seaside, near Del Monte, *Heller* 6654 (C, G, P, S, W), *K. Brandegee* (C); Del Monte, *Coleman* in 1908 (S). While the aspect of a wholly glabrous plant is quite different from that of a very hairy one, I agree with JEPSON that this is deserving of varietal rank only. The peculiar blunt leaves, habit of growth, and other characters are entirely those of *O. cheiranthifolia*. A collection made at Del Monte, by *Patterson & Wiltz* in 1907 (S) is intermediate, being sparsely pubescent.

EXCLUDED AND DOUBTFUL SPECIES

1. *Oenothera alata* Raf., Fl. Ludov., 95. 1817, placed in *Sphaerostigma* by Seringe, D.C., Prodr. **4**:46. 1828; apparently to be referred to *Jussiaea*.

2. *Sphaerostigma andinum* var. *minutum* Nelson, BOT. GAZ. **40**:56. 1905, is *Gayophytum caesium* T. & G., so far as I can tell from the depauperate plants which constitute the type; in any case, it is a *Gayophytum*.

3. *Sphaerostigma angelorum* (S. Wats.) Nelson, BOT. GAZ. **40**:62. 1905, belongs to *Oenothera*, subgenus *Eulobus*.

4. *Sphaerostigma pterospermum* (S. Wats.) Nelson, l. c., 63, is in the subgenus *Chylismia*.

POMONA COLLEGE
CLAREMONT, CALIF.

[*Accepted for publication January 9, 1928*]

RESPIRATION OF THE SOY BEAN[1]

A. L. HAFENRICHTER

(WITH ELEVEN FIGURES)

Introduction

BARNES (2) called attention to the overemphasis which was being placed, especially by botanists, upon the gaseous exchange of respiration. He pointed out the importance of a knowledge of the energy relations of this function, which can be attained only when more is known concerning the materials which furnish the energy and the specific manner in which they furnish it under the various conditions of the environment. This energy is derived, in the higher plants especially, from the organic compounds stored within the cells. It is liberated by hydrolysis and oxidation, and is believed by some to be dependent upon enzymatic reactions. That the carbohydrates and fats are the compounds which furnish the greater part of this energy is recognized by all physiologists. The proteins may furnish energy under certain conditions, but in the light of existing knowledge the amount is never very large. The proteins give by-products, however, which by their presence within the plant may exert a considerable influence upon the rate of metabolism of the carbohydrates and fats.

It has been known for a long time that the stored food materials of seeds undergo a series of changes during germination and development, and that these changes cause qualitative and quantitative differences in the materials subject to metabolism. The manner in which these qualitative and quantitative differences may affect respiration under various conditions has not been fully investigated, nor is it known whether or not the required amount of energy under

[1] Thesis submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy in Botany in the Graduate School of the University of Illinois, 1926.

The writer gratefully acknowledges help in the selection of the problem, aid in the construction of apparatus, and helpful suggestions received from Professor CHARLES F. HOTTES, under whose direction this investigation was conducted.

any given set of conditions is always supplied by a definite metabolic process. It has been demonstrated by animal physiologists, in experiments on metabolism, that it is possible to maintain the same energy relations by substituting qualitatively different foods, provided the caloric values remain constant. Should such substitution be found to occur in higher plants, it would be of importance to know whether it follows definite laws, and in what way it is related to external conditions and the economy of the organism. In this respect it has been shown that some of the lower plants may use only one of two closely related carbohydrates when grown under certain conditions; further, that such plants may utilize different amounts of one food in the presence of different quantities of another. This seems to emphasize the possibility that external as well as internal conditions may determine the kind of respirable materials utilized by the plant as a source of energy.

Historical review

During the germination of seedlings changes are constantly taking place in the various reserve food materials. Since the rate of change varies as development proceeds and is different for each of the several reserves, it would follow that there is a constant alteration in the nature and amount of respirable materials present at any one time. A similar variation would occur in those by-products of metabolism which are not directly respirable, but indirectly exert an influence. From a study of the literature bearing upon this question, it appears that the original composition of the seed may affect these relations.

PRIANISCHNIKOW (**29**) grew *Vicia faba* in distilled water in the dark for forty days. At ten-day intervals he made chemical analyses to determine the changes the reserve foods had undergone. The original seed contained high percentages of protein and starch, but little fatty material. As development progressed there was a decrease of protein-nitrogen, accompanied by an increase in amid- and asparagin-nitrogen. The most rapid change occurred during the first ten days. The same rate of change was noted for the decrease in starch content, whereas soluble carbohydrates increased slightly during the first period and thereafter decreased gradually. The ether

extract, although small at all times, varied as did the soluble carbohydrates. DETMER (4) made similar analyses with *Cannabis sativa*, a seed containing high percentages of fat and protein but no starch. The fat decreased rapidly during the first seven days and more slowly the following three days. After seven days considerable starch was found, but much of this had disappeared at ten days. The amount of protein remained essentially the same, and at no time were soluble carbohydrates found. FRANKFURT (7) obtained much the same result with *Helianthus annuus*, which has the same relative composition, but reported an increase in soluble carbohydrates and a decrease in protein-nitrogen not obtained by DETMER.

Comparative studies of the protein metabolism of *Vicia faba*, *Pisum sativum*, and *Lupinus luteus* were made by PRIANISCHNIKOW (30). The composition of *P. sativum*, according to SCHULZE, STIEGER, and MAXWELL (33), is very similar to that of *Vicia faba*, while *L. luteus* contains a high percentage of protein, considerable fat, but no starch. In all of these protein-nitrogen decreased, at first gradually, then rapidly to a maximum, and after this more slowly. However, at no time in their development was the rate of decrease the same in any of the plants studied. In each case the rate of increase in asparagin-nitrogen paralleled rather closely that for decrease in protein-nitrogen, yet certain differences occurred which indicated that other amino acids were being formed. In the light of the more recent work of THOMPSON (36) and ZLATAROFF (38), such a conclusion seems warranted, although they used different kinds of seeds. Comparison of PRIANISCHNIKOW's results on *L. luteus* with those of MERLIS (20) on *L. angustifolius* indicates that there was a considerable difference in the rate of protein metabolism between these closely related species. SCHULZE (32) believed that such differences might be attributed to differences in the qualitative nature of the proteins in the seed.

MILLER (22) pointed out that different seeds showed a difference in the digestion of fats similar to the difference in protein digestion just discussed. In this article may be found an extensive bibliography and review of the literature. Here especially there seems to have been a relationship between chemical properties of the original reserves, the nature and rate of change, and the products formed.

IVANOW (13) and MAQUENNE (19) attributed this to the proportion of saturated to unsaturated fats.

The qualitative and quantitative changes in the reserve food materials during the development of seedlings may be modified greatly by changes in the environmental conditions. Temperature was found by PRIANISCHNIKOW (31) to influence the rate of protein metabolism in germinating peas. Closer examination of his data indicates that the influence was more marked between eight and thirteen days than at earlier periods. WASNIEWSKY (37), working with wheat seedlings, showed that temperature changes affected the digestion of starch and protein differently. Small changes in temperature at which potatoes were stored were very effective, according to HOPKINS (11), in producing differences in the rate of sugar accumulation. FISCHER (6) demonstrated that the fats stored during the winter in the twigs of the so-called "fat trees" were rapidly converted to starch when subjected to higher temperatures, the rate of change being proportional to the temperature. When again placed at lower temperatures the reverse of this process took place.

It is evident, therefore, that external conditions alter the metabolic processes of plants. The extent to which this is possible seems to depend upon several internal factors, such as the stage of development, composition of the reserve materials, etc. The different results obtained in comparative studies on respiration may be related to such factors, and the effect of the environment on them, but this is still an open question.

The rate of respiration of *Vicia faba*, *Pisum sativum*, and *Lupinus luteus* throughout their development was studied by PRIANISCHNIKOW (30). In each of these he obtained a "grand period" curve, but the respective curves showed clearly that there were individual differences. KUIJPER (17), where will be found a comprehensive review of the literature, determined the effect of temperatures between 0° and 50° C. on the hourly rate of respiration of lupines, peas, and wheat. Differences in the respiration of these plants between certain limits of temperature were not the same as they were between other limits. POURIEWITSCH (27) studied the respiration of seedlings of five species of plants, representing four genera, at different stages in their development. Temperature influ-

enced the value of the respiratory quotient, the effect being more marked in young seedlings than in older ones. GORE (9) determined the effect of temperature on the respiration of different varieties of fruits, and found that they varied even when grown in the same orchard. The difference was more marked at high temperatures than at lower ones. POURIEWITSCH concluded that the effect of temperature on the respiratory quotient was dependent upon the qualitative nature of the nutrient materials in the tissues of the plant. KUIJPER (17) drew essentially the same conclusion. Quantitative chemical analyses were not made in either of these cases.

GERBER (8) argued from his results with flax and castor bean that the value of the respiratory quotient depended upon the "ease" with which the fats were oxidized. IVANOW (14) believed his experiments with sprouting seeds rich in oil showed that temperature exerted a considerable influence upon the coefficient of respiration. His position has been summarized as follows: "This value was said to depend upon external conditions and upon the nature of the plant and was not constant for any group (of conditions?) with oil-containing seeds." DELEANO (3) found that detached leaves of the grape respired only carbohydrates, chiefly starch, during the first 100 hours in the dark. After this there was a marked change in the respiratory process in which the proteins were especially affected. HASSELBRING and HAWKINS (10), BAILEY and GURJAR (1), and HOPKINS (11), working with sweet potatoes, wheat, and Irish potatoes respectively, concluded that the intensity of respiration was correlated with the sugar content, more especially the reducing sugar content. PALLADIN (24) attempted to establish a relation between the intensity of respiration and the content of nitrogen not digestible in gastric juice (protoplasmic nitrogen). He found a better correlation to exist in wheat than in lupine. SPOEHR and MCGEE (34), in their recent work on the respiration of detached leaves of sunflower and "Canada Wonder" bean, grown on nutrient solutions containing different sugars and amino acids, showed a relationship between the intensity of respiration, sugar content, and amino acid content. In general they found that an increase of amino acids increased the rate of respiration when the leaves contained an ample supply of carbohydrates. In the experiments which were conducted at differ-

ent temperatures, 20° and 24° C., the data seem to indicate that the change in the amino acid and sugar content may have been due to the temperature and the amount of the respective substances present at the start. PFEFFER (**25**) was able to demonstrate that the utilization of organic foods by fungi depended upon the quantitative and qualitative relations of these materials in the nutrient solution. He also found that temperature modified the results obtained. POURIEWITSCH (**28**) concluded that these relations were reflected in the value of the respiratory quotient of *Aspergillus niger*, one of the plants used by PFEFFER.

Methods

Two varieties of soy bean, Manchu and Midwest, grown in 1924 under similar field conditions from certified seed, were obtained from the Illinois Agricultural Experiment Station and stored in tin containers in the laboratory until used. Lots of each variety containing carefully selected beans of equal weight were planted in sand of optimum moisture content (45 per cent of the holding capacity), and placed in the constant temperature cases. At the same time a similar lot of each was placed in the drying oven for moisture determination. When the beans had germinated so that the average length of the radicle was approximately 4 cm., the seed coats were removed and 25–30 selected plants from each lot were transferred to paraffined wire nets over 400 cc. of sterilized tap water. The cultures were then placed in the respiration chambers at the respective temperatures at which they were germinated, 15°, 20°, and 25° C. The respiration rate of these (in the dark) was determined in 24-hour intervals until there was evidence of starvation.

Throughout these experiments the aeration method was used. Before gas was collected for analysis, carbon dioxide-free air was drawn through the plant chamber for one hour at such rate that the volume of air was changed at least three times. After this the chamber was connected to an aspirator bottle which served both as an aspirator and as a means for collecting the gas. It contained a specially prepared liquid, furnished by Professor S. W. PARR of the Chemistry Department, which was known to absorb only the slightest trace of carbon dioxide. By means of this aspirator, specially

designed for use in these experiments,[2] it was possible to regulate and maintain a constant rate of aspiration at all times. The rate of aspiration was so adjusted that the concentration of carbon dioxide in the chamber did not exceed 0.5 per cent at any time.

The air drawn into the chamber was first passed through a 40 per cent solution of potassium hydroxide in Winckler tubes (3-foot) to remove the carbon dioxide. A sufficient length of glass tubing was used within the temperature case to bring the temperature of the incoming air to the temperature of the chamber. The intake tube of the chamber extended below the nutrient solution of the culture, so that this was being aerated constantly; hence carbon dioxide, which might have been absorbed by it, was removed by mass action.

The gas collected was analyzed by means of a Morehead burette, according to the method described by PARR and VANDAVEER (23). The volume was determined with a gas meter graduated to hundredths of a liter, but which allowed accurate estimates of one-thousandth part of a liter. This was reduced to 0° C. and 760 mm. mercury pressure. The results of the respiration rate determinations are expressed on the basis of milligrams of CO_2 emitted per hour per gram of original dry weight. In order to make this dry weight basis more absolute, the weight of the seed coats was deducted from the original dry weight of the beans. Since any measure of the stage of development of the plants would be largely arbitrary, it is here expressed as the number of hours following the planting of the seeds.

The respiration chambers used in these experiments were made from a good quality of tin and provided with tightly fitting covers. They were 360 mm. high and had an inside diameter of 160 mm. An intake tube was soldered in near the top of the chamber and an outlet tube near the bottom. Before each series of experiments these chambers were immersed in water and tested for leaks at approximately 100 mm. mercury pressure. They were then disinfected with a strong solution of formalin, rinsed with distilled water, and aerated with a stream of air which had first passed through concentrated sulphuric acid. Adequate precautions were taken throughout to prevent errors in the results due to contamination of the cultures by microorganisms.

[2] To be described in a forthcoming article.

It occasionally became necessary to remove some of the plants from the chamber because of injury, abnormalities of growth, or an indication of infection. Since all of the beans in each culture were of the same weight originally, it was possible to do this and by proper

TABLE I

RATE OF RESPIRATION OF MANCHU AND MIDWEST SOY BEANS AT 25° C.

TIME AFTER PLANTING IN HOURS	CO_2 PER HOUR PER GM. OF ORIGINAL DRY WEIGHT (MG).					
	Manchu			Midwest		
From To	1	2	Average	1	2	Average
72– 96	1.201	1.269	1.235	1.075	1.130	1.102
96–120	1.982	1.963	1.973	2.542	2.744	2.642
120–144	2.191	2.135	2.163	1.386	1.514	1.450
144–168	2.676	1.712	2.194	1.730	2.055	1.892
168–192	1.647	1.576	1.612	1.096	1.747	1.421
192–216	1.020	1.138	1.079	1.450	0.899	1.175
216–240	1.903*	1.253	(1.253)	0.883	0.975	0.929
240–264	1.130†	1.282	(1.282)	0.790	0.930	0.860
264–288	1.186	0.781	0.984	1.258	0.833	1.046
288–312	0.216	0.474	0.345	0.986	0.831	0.909
312–336	.....	0.602	0.602	0.854	0.456	0.655
336–360	.....	0.876	0.876	0.755	0.509	0.642
360–384	.....	0.615	0.615	0.680	0.416	0.548
384–408	.....	0.441	0.441	0.603	0.925	0.764
408–432	.....	0.244	0.244	0.643	1.048	0.845
432–456	0.285	0.513	0.399	1.087	1.197	1.142
456–480	0.361	0.551	0.406	1.134	0.663	0.898
480–504	0.546	0.775	0.661	1.210	0.481	0.846
504–528	0.381	0.596	0.488	.....	0.907	0.907
528–552	.....	0.783	0.783	.....	.....	.....
552–576	.....	0.748	0.748	.....	.....	.....
576–600	.....	0.713	0.713	.....	.....	.....

* Temperature of case up to 30° C. during the night.

† Temperature of case down to 20° C. for four hours.

Neither of these values considered in the average.

calculations to retain the dry weight basis. It was seldom necessary to remove more than a few, so that the space relations were not appreciably disturbed.

Results

VARIATION IN RESPIRATION.—The results of the respiration rate determinations are found in tables I, II, and III, and are shown graphically in figs. 1, 2, and 3. It will be seen that there is great variation in the rate of respiration of either variety of soy bean

TABLE II

RATE OF RESPIRATION OF MANCHU AND MIDWEST SOY BEANS AT 20° C.

TIME AFTER PLANTING IN HOURS	CO_2 PER HOUR PER GM. OF ORIGINAL DRY WEIGHT (MG.)		TIME AFTER PLANTING IN HOURS	CO_2 PER HOUR PER GM. OF ORIGINAL DRY WEIGHT (MG.)	
From To	Manchu	Midwest	From To	Manchu	Midwest
96–120	1.218	1.137	408–432	1.150	0.454
120–144	1.435	1.465	432–456	0.658	0.474
144–168	1.984	1.840	456–480	1.248	0.791
168–192	2.426	2.046	480–504	0.371	0.371
192–216	2.199	1.278	504–528	0.482	0.313
216–240	1.385	0.865	528–552	0.829	0.674
240–264	0.883	1.410	552–576	0.984	0.621
264–288	0.939	1.147	576–600	0.786	0.820
288–312	0.962	1.057	600–624	0.737	0.653
312–336	0.724	0.480	624–648	0.775	0.454
336–360	0.856	0.480	648–672	*	0.588
360–384	0.414	0.687	672–696		0.555
384–408	1.275	0.821			

* Culture too badly contaminated for further use.

TABLE III

RATE OF RESPIRATION OF MANCHU AND MIDWEST SOY BEANS AT 15° C.

TIME AFTER PLANTING IN HOURS	CO_2 PER HOUR PER GM. OF ORIGINAL DRY WEIGHT (MG.)		TIME AFTER PLANTING IN HOURS	CO_2 PER HOUR PER GM. OF ORIGINAL DRY WEIGHT (MG.)	
From To	Manchu	Midwest	From To	Manchu	Midwest
240–264		0.438	696– 720	0.654	
264–288	0.786		720– 744	0.435	0.321
288–312		0.814	744– 768	0.195	0.271
312–336	0.416		768– 792	0.122	0.415
336–360		0.782	792– 816	0.306	0.293
360–384	0.248		816– 840	0.105	0.463
384–408		1.066	840– 864	0.321	0.483
408–432	0.281		864– 888	0.365	0.898
432–456		1.174	888– 912	0.624	1.358
456–480	0.265		912– 936	0.549	0.651
480–504		0.530	936– 960	0.396	0.224
504–528	0.233		960– 984	0.439	†
528–552	0.243	0.643	984–1008	0.547	0.174
552–576	0.389		1008–1032	0.510	0.162
576–600	0.373	0.803	1032–1056	0.307	0.201
600–624	0.390		1056–1080	‡	0.074
624–648	0.349	0.428	1080–1104		0.344
648–672	0.275		1104–1128		0.093
672–696	0.577	*			

* Value too small to measure accurately.

† Accident to burette made reading uncertain.

‡ Culture too badly contaminated for further use.

throughout its development. There is no regular periodicity in this variation, nor do the fluctuations show consistent similarity at all temperatures, even when allowance is made for the relative differ-

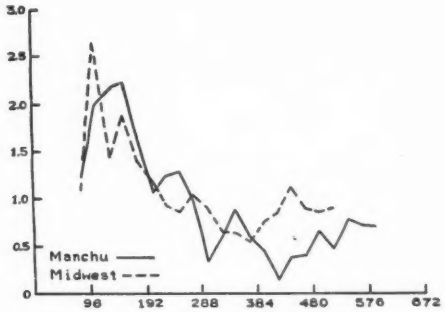


Figure 1

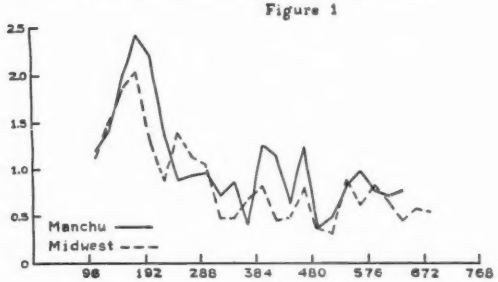


Figure 2

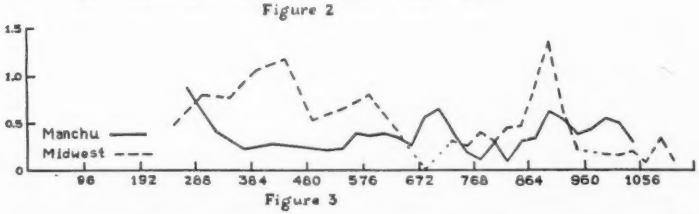


Figure 3

FIGS. 1–3.—Fig. 1, rate of respiration of Manchu and Midwest soy beans at 25° C.: abscissas represent time in hours; ordinates represent mg. CO_2 emitted per hour per gm. of original dry weight of seeds; values from table I; fig. 2, rate of respiration of Manchu and Midwest soy beans at 20° C.: abscissas represent time in hours; ordinates represent mg. CO_2 emitted per hour per gm. of original dry weight of seeds; values from table II; fig. 3, rate of respiration of Manchu and Midwest soy beans at 15° C.: abscissas represent time in hours; ordinates represent mg. CO_2 emitted per hour per gm. of original dry weight of seeds; values from table III.

ence in the rate of development. The greatest variation in rate is found to occur during the early periods of development (excepting that of the Manchu variety at 15° C.), and again immediately preceding the time when the majority of the plants in the culture succumb to starvation. The two varieties differ with respect to the degree and manner of variation in the rate of respiration. During one period of development that of the one variety fluctuates to a greater extent and in a different manner from that of the other. These differences are often entirely reversed at other periods, or at least greatly changed. The same is true, in general, in regard to the relative intensities of respiration.

TEMPERATURE AND RESPIRATION.—Comparison of the results obtained at different temperatures indicates that small differences in temperature may have a greater influence upon the respiration of one variety of a species than upon another. At 25° C. the intensity of respiration is, in general, higher and tends to vary less in the Midwest variety than in the Manchu. The rate of respiration of the Midwest at 20° C. fluctuates less but is, with the exception of one 72-hour period, lower than that of the Manchu. At 15° C. the Midwest variety not only shows a greater variation in its respiration rate, but a much more intensive respiration at nearly all periods during its development. Each variety has a well defined maximum during the early stages of development at 25° and 20° C.; at 15° this is found only in the Midwest variety. During the early stages of development, and again just before exhaustion, the difference in the respiration of these varieties is much greater at 25° and at 15° than at 20° C.

RESPIRATION AND DRY WEIGHT LOSS.—Since the results of the respiration rate determinations are expressed on the basis of the original dry weight of the seeds, it might be argued that the differences obtained would be less if the dry weight of the seedlings at the beginning of each determination was used as the basis. A preliminary experiment was made to test this point. A large number of plants were grown from seeds of equal weight as just described. Ten plants were removed from the cultures at equal periods of time, every 48 hours at 25°, and every 72 hours at 20° C., and dried to constant weight in the drying oven. The results of this experiment

are summarized in table IV and shown graphically in figs. 4 and 6. It is realized that the error of these results may be quite large, due to the small number of plants used, yet the data allow certain conclusions. At 25° C. the actual loss in dry weight by both varieties, during any period, is as nearly similar as is the rate of loss. At 20° C. the actual loss in dry weight for any period is greater in the Manchu than in the Midwest variety. The differences in the respira-

TABLE IV

LOSS OF DRY WEIGHT BY MANCHU AND MIDWEST SOY BEANS AT 25° AND 20° C.; VALUES EXPRESS AVERAGE OF 10 PLANTS

TIME AFTER PLANTING IN HOURS	AVERAGE PERCENTAGE LOSS IN DRY WEIGHT OVER ORIGINAL DRY WEIGHT OF SEEDS			
	25° C.		20° C.	
	Manchu	Midwest	Manchu	Midwest
0	0	0	0	0
72	4.48	1.85	.....	.....
96	.....	.....	5.75	3.45
120	6.08	8.21	.....	.....
168	9.84	10.41	12.74	7.76
216	12.84	14.38	.....	.....
240	.....	.....	16.70	9.51
264	14.27	(21.44)*	.....	.....
312	16.46	17.03	20.06	17.03
360	18.83	21.00	.....	.....
384	.....	.....	22.03	18.79
408	19.96	23.03	.....	.....
456	.....	.....	24.68	24.97

* Value probably due to error as considerable sand adhered to roots.

tion of the two varieties at either temperature, therefore, would be magnified rather than reduced if based upon the dry weight of the seedlings at the beginning of each determination. At 20° the relative difference obtained by this method of calculation would be increased more than at 25° C., for the reasons already mentioned.

RESPIRATION AND GROWTH.—It was thought that the variation in the rate of respiration might in some way be related to the periodicity in the rate of growth, and that this might account for some of the differences in the respiration of the varieties. Accordingly, when the plants were removed from the cultures for dry weight determinations, measurements were made to determine the increment of

growth, both of the hypocotyl and epicotyl. The average increment of growth of ten plants is given in table V. These values are reduced

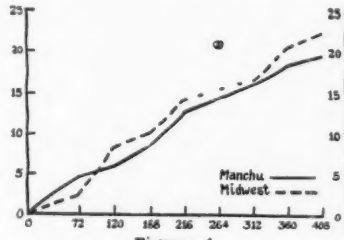


Figure 4

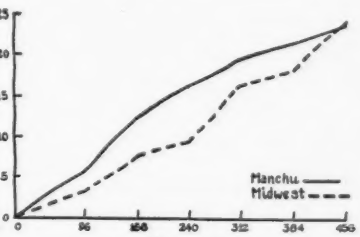


Figure 6

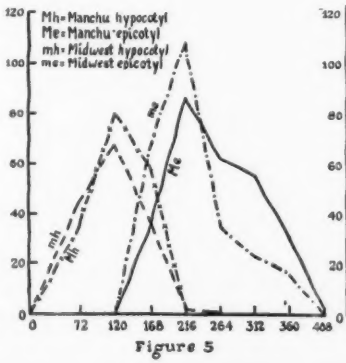


Figure 5

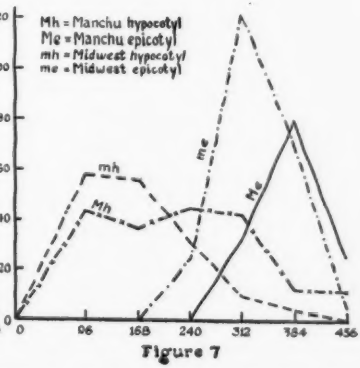


Figure 7

FIGS. 4–7.—Fig. 4, rate of loss of dry weight by Manchu and Midwest soy beans at 25° C.: abscissas represent time in hours; ordinates represent percentage loss over original dry weight of seeds; values from table IV; fig. 5, rate of growth of Manchu and Midwest soy beans at 25° C.: abscissas represent time in hours; ordinates represent increment of growth in mm.; values from table V; fig. 6, rate of loss of dry weight by Manchu and Midwest soy beans at 20° C.: abscissas represent time in hours; ordinates represent percentage loss over original dry weight of seeds; values from table IV; fig. 7, rate of growth of Manchu and Midwest soy beans at 20° C.: abscissas represent time in hours; ordinates represent increment of growth in mm.; values from table V.

to graphs in figs. 5 and 7. As already mentioned, the possibility of error is large. It will be seen, however, that the rate of growth of each part of the shoot increases to a maximum and then decreases,

yet noticeable differences seem to exist between the two varieties. These differences are more apparent at 20° than at 25° C. A direct correlation between the growth rate and respiration does not seem possible in the case at hand. Neither is it likely that the differences

TABLE V

GROWTH IN MM. OF MANCHU AND MIDWEST SOY BEANS AT 25° AND 20° C.; VALUES EXPRESS AVERAGE OF 10 PLANTS

TIME AFTER PLANTING IN HOURS	MANCHU				MIDWEST			
	HYPOCOTYL		EPICOTYL		HYPOCOTYL		EPICOTYL	
	Length	Growth	Length	Growth	Length	Growth	Length	Growth
	Temperature 25° C.							
0	0	0	0	0	0	0	0	0
72	35	35	0	0	45	45	0	0
120	115	80	0	0	113	68	0	0
168	174	59	36	36	148	35	68	68
216	165	(0)*	123	87	150	2	177	109
264	179	(0)	186	63	143	(0)*	212	35
312	180	(0)	242	56	152	(0)	235	23
360	176	(0)	274	32	149	(0)	252	17
408	176	(0)	276	2	148	(0)	241	(0)*
	Temperature 20° C.							
0	0	0	0	0	0	0	0	0
96	43	43	0	0	58	58	0	0
168	80	37	0	0	114	56	0	0
240	125	45	0	0	145	31	24	24
312	167	42	32	32	155	10	146	122
384	180	13	112	80	159	4	215	69
456	192	12	136	24	154	(0)*	220	5

* Growth increment considered as 0 due to the possible error resulting from the use of small numbers

in the respiration rate of the two varieties might be explained on the basis of differences in the rate of growth.

Discussion

Soy beans were selected for use in this investigation because they possess several advantages from an experimental point of view. The inherent nature of most autotrophic plants makes difficult the kind of experimentation employed by the animal physiologist to determine the fundamental principles of respiratory metabolism. Be-

cause of this it has been customary to employ highly artificial methods, or to use plants which were known to have different kinds and amounts of reserve food materials. Either of these methods may lead to an incorrect interpretation of the respiratory metabolism of the plant, as will be shown later. The use of soy bean varieties overcomes several of these difficulties. According to PIPER and MORSE (**26**), soy bean seed contains 15–25 per cent fat, 30–45 per cent protein, and no starch if the seed is properly matured. The limited number of reserve food materials in this seed is of distinct advantage in comparative studies of respiratory metabolism. Traces of carbohydrates have been found in soy bean seed, but the authors referred to consider the available data widely divergent and conflicting. Several instances are cited where various investigators claim to have found 2 to 3 per cent of sugar, traces to 4 per cent of pentosans, and other carbohydrates in small quantities. In any case the amounts are comparatively small, and might be expected in any of the seeds generally employed in investigational work. Another advantage lies in the fact that the composition of the seed of soy bean varieties varies quantitatively. This makes possible the selection of seeds of varieties which contain different amounts of the two principal reserves. The relative amounts of the respective reserves are altered by cultural conditions, as was shown by STARK (**35**). Under similar field conditions, one variety may be designated as having a "low oil–high protein" seed and another variety as "high oil–low protein" seed. When the same varieties are grown under dissimilar field conditions this might be reversed. The seeds used were chosen with this in view. It will be shown later that the use of the two varieties of soy bean chosen largely eliminated the possibility of the reserve materials varying qualitatively.

VARIATION IN RESPIRATION.—As already pointed out, there is a great variation in the rate of respiration during the development of soy beans in the dark. In general the variations are characterized by rapid increases in rate, which are followed by gradual decreases, and by the absence of regular periodicity. In this respect the results differ quite widely from those obtained by PRIANISCHNIKOW (**30**), and from the conclusions he draws from the work of others (RISCHAWI, MAYER, etc.). The rate of respiration in their studies showed no

marked variations. They found the rate to increase gradually to a maximum, and then to decrease gradually as the reserve materials were depleted. When variations were obtained they were always slight. The maximum respiration was found by them to occur late in the development of the seedlings. In the present study, aside from the variations mentioned, the maximum rate of respiration occurs during the first stages of development, with the exception of that of the Manchu variety at 15° C. This difference in results might be due to two things. It might be attributed to the influence of the small amount of carbohydrates present in the seeds. This is hardly possible, however, because the greater part of these carbohydrates has been shown to be pentosans. Wheat has been shown by LE CLERC and BREAZEALE (18) to contain as much as 7.3 per cent of this material. RISCHAWI used this plant in his studies, and obtained no great increase in the rate of respiration during the early stages of development. Further, all of the chemical analyses made on development of seedlings in the dark indicate that the most rapid change in the several reserve foods occurs during the early periods of development. This would obscure the effects of the small amount of carbohydrates present in soy beans. Since the differences are not likely to be due to the pentosans present, they might be attributed to the differences in the method of expressing results. In all of the early works mentioned, the rate of respiration was expressed as the milligrams of carbon dioxide given off by a certain number of plants per hour. This method of expression, unless the dry weight of the seeds is identical, allows considerable error when comparative results are desired.

The variation in the respiration rate of the soy bean varieties is more marked at some temperatures than at others. The two varieties differ from each other especially in this respect. At 25° C. both varieties show the greatest fluctuation at the beginning and again near the end of the development, but at 20° the rapid change near the end of development is lacking in the Midwest variety. At 15° there is no marked increase in the respiration of the Manchu variety during the early periods. The Midwest variety shows a rapid increase both near the beginning and again near the end of its development at this temperature. This does not seem to bear out the conclusion

of POURIEWITSCH (27) that the effect of temperature on respiration is more marked in early stages of development. GORE (9) found that the difference in the respiration of varieties of fruits was more marked at high temperatures than at lower ones. This is not the case with the soy bean varieties used in this investigation. It can be concluded, therefore, that the effect of temperature upon the respiration of plants may be as marked during the early periods of development as during the later periods. Also, that the effect of temperature on respiration is as different for varieties of the same species as it is for different species.

RESPIRATION AND COMPOSITION.—The results obtained by the methods here used would indicate that certain revisions in the current conception of the relation between respiration and chemical composition of the reserves are necessary.

It has been believed, as was shown earlier in this paper, that differences in the respiration of plants depend upon differences in the reserve food materials in the tissues. These conclusions were drawn from results obtained by the use of different species of plants, and often by the use of different genera. If conclusions are to be drawn concerning the effect of quantitative differences in the reserve materials, it seems imperative that plants be selected for experimentation in which these quantitative differences are not masked by differences of a qualitative nature. Concerning the importance of this consideration, the physiologist is at present in a position to make certain assumptions. From the work that has been done on the chemical changes accompanying the germination of fatty seeds and the development of seedlings, it is quite certain that qualitative differences in the reserve materials have a great effect upon the quantitative (and qualitative) nature of the by-products found at different stages of development. It can be assumed with some assurance that the proteins of seeds, especially of different genera of plants, are quite specific. This hypothesis is at the very foundation of the well known precipitin tests which recently have been introduced into botanical investigations by MEZ and his students (21). It is also the basis of the work of SCHULZE (32) in his investigation of the relationship between the qualitative nature of the proteins of seeds and that of the protein by-products found in the seedlings.

The assumption that the qualitative nature of the reserve materials in the seeds of the two varieties is the same has considerable basis in fact. It follows that they differ in composition only quantitatively. According to the data of STARK (**35**), the Midwest variety has a "low oil–high protein" seed, and the Manchu a "high oil–low protein" seed when grown under similar field conditions. Actual analysis of the seed of the varieties used in this study showed that the Midwest contained 39.37 per cent protein and the Manchu 32.19 per cent protein per unit dry weight.

The characteristics of the respiration of these varieties have been pointed out repeatedly. If differences in their respiration are to be explained on the basis of quantitative differences in the reserve food materials, several difficulties are encountered. In the first place, since the fats are the original source of the respirable materials, the fact that the intensity of respiration of the Midwest variety (low oil–high protein) is, in general, higher than the Manchu (high oil–low protein) at 25° and at 15° C. would be difficult of explanation. Secondly, KUIJPER (**17**) concluded that the change from one characteristic respiration rate to another was more marked at lower temperatures in those seeds having a high protein content. If this be true, the intensity of respiration should be consistently lower in the Midwest variety, which has the higher protein content. This is not the case. Moreover, the variation in the respiration of the Manchu variety is least at 15° C. (fig. 3), which does not support the conclusion mentioned. Lastly, POURIEWITSCH (**27**) believed that the effect of temperature upon the respiratory quotient depends upon the qualitative nature of the nutrients in the tissues of the plants. The results obtained by the writer contradict this statement. It might be argued that the measure of respiratory activity was not the same as that used by POURIEWITSCH. This is of no great consequence, however, since FERNANDES (**5**) has shown by very carefully performed experiments that the production of carbon dioxide and the absorption of oxygen by developing seedlings parallel each other closely. Further, the results of POURIEWITSCH must be taken with some reservation, since the checks he used showed abnormally wide variations, 0.11 and 0.54, 0.48 and 0.13, 0.35 and 0.88, for the values of the quotient.

In the discussion of the literature bearing on the changes which take place in the several reserve food materials during the development of seedlings in the dark, it was shown that the greatest change in any of these compounds occurs during the early periods of development. After this the rate of change of any one of them was continuous and gradual, or showed only slight variation. The lack of periodic changes in these materials is the chief characteristic of this early work. This was also shown to be a feature of the respiration rate determinations made on the same plants. The opinions of HASSELBRING and HAWKINS (**10**), BAILEY and GURJAR (**1**), and HOPKINS (**11**) were cited to show that any external conditions which caused a rapid accumulation of respirable materials also caused rapid changes in the rate of respiration. Accordingly, when the results of the respiration rate determinations are considered with respect to directly respirable materials, it appears that the changes in such materials in developing seedlings are not gradual; or, if gradual, that the plant respires different materials at different stages of its development. If either of the above premises should be proved correct, the reactive nature of the protoplasm would be emphasized, and support lent to the idea of PFEFFER (**25**) that there is an "election" of organic nutrients by the plant, and to the idea of POURIEWITSCH (**28**) that this election is reflected in respiration. PFEFFER also believed that environmental conditions, especially temperature, modified the results obtained. This is corroborated by the results obtained in this investigation.

If it be permissible to apply the work of FISCHER (**6**) to the results obtained with soy beans at 15° C., one of two things is evident. Either the conversion of fats to respirable materials is extremely slow, especially in the Manchu variety, or those products which are formed are not respired by the plants. This point awaits clarification, as little is known at present concerning the digestion of fats in developing seedlings at low temperatures. If the first step in the conversion of fats is the production of starch, which is not unlikely from the results of FISCHER and DETMER, consideration would have to be given to the work of HUERRE (**12**), who showed that the cardinal temperatures for the activity of maltase of one variety of maize were considerably lower than that for another variety. Such a possibility

strengthens the proposition that the reactive nature of the protoplasm, rather than the chemical composition as such, is at play in respiratory metabolism. In contradistinction to this, the suggestion might be derived from FISCHER's work that there is a temperature at which the formation of starch from fat, and the reverse of this process, are at equilibrium. This in no way minimizes the proposition already set forth. If it did the respiration rate of the two varieties should at least parallel each other at 15° C., which is not the case.

RESPIRATION AND STARVATION.—The characteristic of respiration just preceding the exhaustion of the seedlings is significant in several ways. Its prevalence at all temperatures, regardless of varietal differences, indicates that the plants act specifically when this period is reached. This has not been shown heretofore, so far as the writer is aware, or at least has not been emphasized. The supposition might be offered that certain by-products of metabolism which have accumulated are influencing the respiratory processes, either directly or indirectly, at this time. On this basis alone it would be difficult to account for differences in the respiration of the two varieties. Still more difficult would be the explanation of the inconsistencies of these differences at all temperatures. It has been demonstrated repeatedly that the intensity of respiration of all parts of the plant decreases as the tissues become older. KIDD, WEST, and BRIGGS (16) reviewed the principal literature bearing on this question, and presented evidence in support of the fact that even the meristematic tissues of plants showed a decrease in respiratory intensity as the plant increased in age. This indicates that the protoplasm of plants undergoes some change which reduces its ability to respire the reserve materials, which, under the conditions of their experiments, were increasing in amount. It therefore seems inconsistent to argue that chemical composition is alone responsible for respiratory activity. This is especially true with respect to the supposition concerning the effect of the accumulation of by-products. However, it is clear that the results of a protoplasmic change in the plants used in the present investigation lead to an increased respiratory activity. This is not in accord with the results obtained by the other investigators.

The differences in the respiration of the two varieties at the various temperatures used allows the conclusion that temperature may have as great an effect during the later periods of development as it has during the early ones. This is contrary to the conclusions of POURIEWITSCH (**27**).

RESPIRATION AND GROWTH.—Although the data presented are insufficient to allow definite conclusions, there seems to be no direct relation between respiration and growth as measured by the increase in length of the parts of the shoot; neither is such a relation evident between the periodicity of growth and that of respiration. Should changes in the intensity of respiration precede or follow changes in the growth rate, a synchronism between the curves of respiration and growth would be expected. This is not apparent in the results obtained. Considering the growth rate of the entire shoot instead of that of its parts, it can be said that the maximum rate of respiration is reached earlier in the development of the plants than is the maximum rate of growth. It will be noted, however, that the interval between the two maxima is greater at 20° than at 25° C. Consequently, the functional interactions which determine growth on the one hand and respiration on the other are affected differently by the same change in environmental conditions.

RESPIRATION AND AMINO ACIDS.—Thus far in this comparative study, consideration has been given only to the possible interrelationship between respiration and the reserve materials which are directly respirable. This restricted comparison would be open to criticism, since it has been shown that the by-products of the reserves which are, under ordinary conditions, not directly respirable may influence respiration. It was shown earlier in this paper (SPOEHR and MCGEE **34**) that an increase in the amino acid content of excised leaves increased the rate of respiration when the leaves contained an ample supply of carbohydrates. This was especially true when the leaves were "fed" sugars and amino acids. Concerning the effect of the natural accumulation of amino acids on respiration, these writers expressed themselves as follows:

> Undoubtedly the carbohydrate supply alone does not determine the rate of respiration, but there is necessary an accessory factor which aids the successive chemical reactions constituting this process. That the amino acids act

in this stimulating manner is established by the experiments here described, and the point naturally suggests itself that under normal conditions in the dark, when carbohydrate content decreases and the amino acids increase, there is a similar stimulating action which tends to maintain a relatively higher respiration rate. . . . . It appears that the natural accumulation of amino acids is just as effective in stimulating respiratory activity as when amino acids are fed to the leaves.

From this it would seem that the consideration of these substances is paramount to any study of respiratory metabolism. Fortunately such a study was being carried on simultaneously in the laboratory of plant physiology at the University of Illinois. The plants used for this study were grown from the same seed as those used in the respiration studies, and under the same controlled conditions. In figs. 8 and 10 will be found the results of the amino acid determinations, made by the Van Slyke method, kindly furnished the writer by Dr. ORTON K. STARK from unpublished data. In order clearly to show the relationship between amino acids and respiration, the results obtained in the respiration studies are again plotted in figs. 9 and 11. It is necessary to point out that the determinations of the amino acids were carried out further than was possible in the respiration studies. For this reason, the time at which the cultures used in the amino acid determinations showed the same degree of exhaustion as was evident when it was necessary to terminate the respiration studies is indicated on the amino acid graphs.

Inspection of the graphs for the amino acid content shows that there is as great a variation in the amino acid content as there is in the rate of respiration. The lack of regular periodicity is equally evident, as is the absence of similarity between the curves of the two varieties. A comparison of the curve for the amino acid content of either variety with that for respiration, shows that in general there is no direct relation between amino acid content and respiration. This is especially apparent during the early stages of development, 72 to 120 hours at 25°, and 96 to 240 hours at 20° C. It will be seen that during the later periods an increase in the rate of respiration is accompanied by a decrease in the amino acid content, and vice versa. There are a few exceptions to this generalization at both temperatures, but a closer inspection of the graphs reveals the

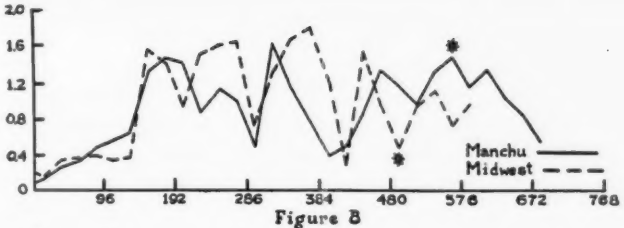


Figure 8

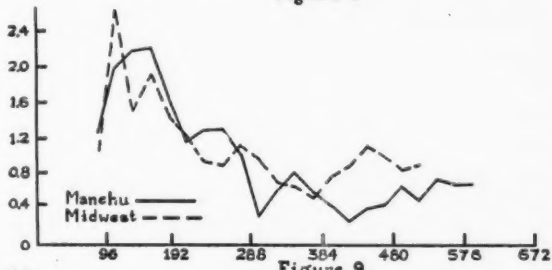


Figure 9

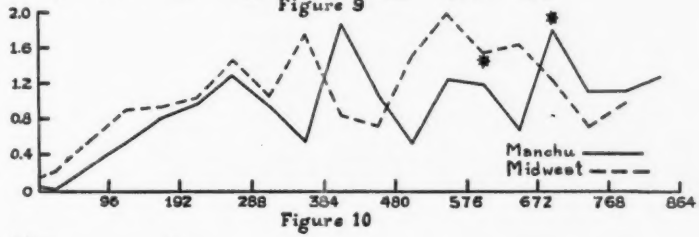


Figure 10

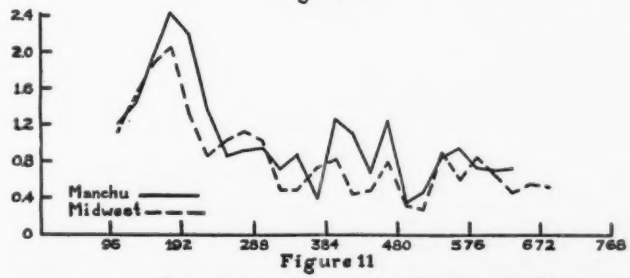


Figure 11

FIGS. 8–11.—Fig. 8, amino acid content of Manchu and Midwest soy beans at 25° C.: abscissas represent time in hours; ordinates represent percentage of original dry weight which is amino acids; values from unpublished data at University of Illinois; asterisk indicates time when amino acid cultures reached stage of development necessary to discontinue respiration studies; fig. 9, rate of respiration of Manchu and Midwest soy beans at 25° C.: abscissas represent time in hours; ordinates represent mg. CO_2 emitted per hour per gm. of original dry weight of seeds; values from table I; fig. 10, amino acid content of Manchu and Midwest soy beans at 20° C.: abscissas represent time in hours; ordinates represent percentage of original dry weight which is amino acids; values from unpublished data at University of Illinois; asterisk indicates time when amino acid cultures reached stage of development necessary to discontinue respiration studies; fig. 11, rate of respiration of Manchu and Midwest soy beans at 20° C.: abscissas represent time in hours; ordinates represent mg. CO_2 emitted per hour per gm. of original dry weight of seeds; values taken from table II.

fact that when, for example, an increase in respiration is accompanied by an increase in amino acid content, the rates of the respective increases vary widely from one another. For this reason these exceptions are not regarded as significant. When the graphs expressing the rate of respiration of the two varieties are compared with those of the amino acid content, it is seen that the differences in the respiration are concomitant with differences in the amino acid content. It is significant, however, that when the rate of respiration of the one variety is higher or lower than that of the other, its amino acid content is respectively lower or higher. The slight exceptions to this, especially at 25° C., may be disposed of in the same manner as those just referred to. At 20°, where in a few instances the exceptions are more marked, no definite conclusions can be drawn concerning them. The analyses of the amino acid content were made only at 48-hour intervals at this temperature. The exceptions mentioned might be attributed to this, since the rate of respiration shows a considerable change in 24 hours at 20° C.

From these results it can be concluded that the normal accumulation of amino acids in plants grown in the dark is incidental, rather than necessary to respiration. At the best it is highly improbable that their accumulation is in any way essential to the economy of the plant in maintaining its respiratory intensity.

It could be argued, from the results of SPOEHR and MCGEE, that the decreased supply of carbohydrates in the seedlings, especially during the later periods of development, obscured the stimulating effect of the amino acids. On this basis it would be difficult to account for the fact that, during the early periods of development, the relative intensity of the respiration is in inverse relation to the relative amino acid content. During this period it is reasonable to expect, from chemical analyses which have been made by others, that the supply of carbohydrates is "ample."

The results of the respiration studies reported in this paper and those of amino acid content made on the same plants are significant in another way. The variation in the rate of respiration is rapid, great changes occurring in 24 hours. Equally great are the changes in the amino acid content during a similar period. In the discussion of the literature relative to the changes which took place in the

various reserve materials during the development of seedlings, it was shown that the changes in the several reserves were progressive and comparatively gradual. Thus it was thought that the protein content decreased gradually and the amino acids increased similarly. The same general conclusion was drawn by the various writers concerning the other reserves. Analyses were made, in the majority of these cases, at intervals of several days. From the study of respiration and amino acids reported in this paper, it is reasonable to conclude that the changes in any of the reserve foods are not gradual when the interval of determination is sufficiently short, and that a correct interpretation of this phase of metabolism requires further study.

Summary

1. The two varieties of soy bean used in this investigation were selected in such a manner that the seeds varied in composition only quantitatively.

2. It is shown by comparative study of the two varieties that: (1) the rate of respiration, at all temperatures, varies greatly during the development of the seedlings without indication of periodicity; (2) there is a great difference between the two varieties with respect to the intensity and the fluctuation of the rate of respiration; and (3) the maximum rate of respiration occurs early in the development of the seedlings, with the exception of that of the Manchu variety at 15° C.

3. Temperature has a great influence upon the degree and relative rate of variation in respiration, but the effect is not the same at different stages of development, nor is it the same for each variety.

4. The effect of temperature on respiration is as markedly different in the two varieties as was that reported by others for different species of plants.

5. The conclusion of others, that differences in the respiration of different plants can be explained on the basis of quantitative differences in the reserve food materials, is not supported by the results obtained in this investigation.

6. Evidence is presented which supports the theory of PFEFFER that plants show an "election" of organic nutrients, and the results of POURIEWITSCH that this election is reflected in respiration.

7. Soy beans grown in the dark show a marked increase in the rate of respiration preceding the complete exhaustion of the plants. This has not been demonstrated previously.

8. No direct relation between respiration and growth seems to exist from the data obtained in this investigation.

9. The accumulation of amino acids in soy bean seedlings grown in the dark is incidental, rather than necessary to respiration. No evidence was obtained, under the conditions of these experiments, to support the theory that the amino acids stimulate respiration.

10. Evidence is presented to show that the changes in the reserve food materials in developing seedlings is not progressive and gradual, as heretofore has been supposed.

BAKER UNIVERSITY
BALDWIN, KAN.

[*Accepted for publication November 11, 1927*]

LITERATURE CITED[3]

1. BAILEY, C. H., and GURJAR, A. M., Respiration of cereal plants and grains. II. Respiration of sprouted wheat. Jour. Biol. Chem. **44**:5–7. 1920.
2. BARNES, C. R., The theory of respiration. BOT. GAZ. **31**:81–98. 1905.
3. DELEANO, N. T., Studien über den Atmungsstoffwechsel abgeschnittener Laubblätter. Jahrb. Wiss. Bot. **51**:541–592. 1912.
4. DETMER, W., Vergleichende Physiologie des Keimungsprocesses. pp. 565. Jena: G. Fischer. 1880.
5. FERNANDES, D. S., Aerobe und Anaerobe Atmung bei Keimlinge von *Pisum sativum*. Recueil Trav. Bot. Neerl. **20**:107–256. 1923.
6. FISCHER, A., Beiträge zur Physiologie der Holzgewächse. Jahrb. Wiss. Bot. **22**:73–160. 1891.
7. FRANKFURT, S., Über die Zusammensetzung der Samen und der etiolierten Keimpflanzen von *Cannabis sativa* und *Helianthus annuus*. Landw. Versuchsst. **43**:143–182. 1893.
8. GERBER, C., Étude comparée de la respiration des graines oléagineuses pendant leur développement et pendant leur germination. Rélation chimiques dont la graine est la siège. Acts Ier Cong. Internat. Bot. Paris **1900**: 59–101. 1900.

[3] The following articles have been published since this paper went to press:

STARK, ORTON K., The protein metabolism of the soy bean. Amer. Jour. Bot. **14**:532–547. 1927.

HOTTES, C. F., and HAFENRICHTER, A. L., A constant rate aspirator. Science. **67**:320–322. 1928.

9. GORE, H. C., Studies on fruit respiration. U.S. Dept. Agric., Bur. Chem. Bull. 142. 1–40. 1911.
10. HASSELBRING, H., and HAWKINS, L. A., Respiration experiments with sweet potatoes. Jour. Agric. Res. **5**:509–517. 1915.
11. HOPKINS, E. F., Relation of low temperature to respiration and carbohydrate changes in potato tubers. BOT. GAZ. **76**:311–325. 1924.
12. HUERRE, R., Sur la maltase du maïs. Compt. Rend. Acad. Sci. Paris **148**: 300; 500. 1909.
13. IVANOW, S. L., Über die Verwandlung des Oels in der Pflanzen. Jahrb. Wiss. Bot. **50**:375–386. 1912.
14. ———, The influence of oil reserves of seeds and of temperature on the respiration coefficient. Zhur. Opytn. Agron. **14**:75–87. Cited in Exp. Sta. Rec. **29**:525. 1913.
15. JEGOROW, M., Über Stoffmetamorphose dei der Samenkeimung von *Curcubita maxima*. Ann. l'Institut Agron. Moscou. Annee X. Libre 2. 1904. Cited in Bot. Centralbl. **101**:597. 1906.
16. KIDD, F., WEST, C., and BRIGGS, G. E., A quantitative analysis of the growth of *Helianthus annuus*. I. The relation of the plant and of its parts throughout the life cycle. Proc. Roy. Soc. London B **92**:368–384. 1921.
17. KUIJPER, J., Über den Einfluss der Temperatur auf die Atmung der höheren Pflanzen. Recueil Trav. Bot. Neerl. **7**:121–140. 1910.
18. LECLERC, J. A., and BREAZEALE, J. F., Translocation of plant food and elaboration of organic plant material in wheat seedlings. U.S. Dept. Agric., Bur. Chem. Bull. 138. 1–32. 1911.
19. MAQUENNE, L., Sur la changements de composition qu'éprouvent les graines oléagineuses au cours de la germination. Compt. Rend. Acad. Sci. Paris **127**:625. 1898.
20. MERLIS, M., Zusammensetzung der Samen und der Etiolierten Keimpflanzen von *Lupinus angustifolius*. Landw. Versuchsst. **48**:419–454. 1898.
21. MEZ, C. et al, Sero-diagonische Studien. Beitr. Biol. Pflanzen **12**:155, 214, 216, 218, 347; **14**:145. Bot. Archiv. **1**:2, 81, 129, 177; **2**:57, 177; **5**:413; **6**:421; **7**:9; **8**:3. 1913–1926.
22. MILLER, E. C., A physiological study of the germination of *Helianthus annuus*. II. The oily reserves. Ann. Botany **26**:889–901. 1912.
23. PARR, S. W., and VANDAVEER, F. E., The analysis of fuel gas. Univ. Ill. Engin. Exp. Sta. Cir. **12**:1–41. 1924.
24. PALLADIN, M. W., Recherches sur la corrélation entre la respiration des plantes et les substances azotées actives. Rev. Gen. Bot. **8**:225–248. 1896.
25. PFEFFER, W., Über Election organischer Nährstoffe. Jahrb. Wiss. Bot. **28**:205–286. 1895.
26. PIPER, C. V., and MORSE, W. J., The soy bean. xv+329. New York: McGraw Hill. 1923.
27. POURIEWITSCH, M. K., Influence de la température sur la respiration des plantes. Ann. Sci. Nat. Bot. Ser. 9. **1**:1–32. 1905.

28. POURIEWITSCH, M. K., Physiologische Untersuchungen über Pflanzenathmung. Jahrb. Wiss. Bot. **55**:573–610. 1900.
29. PRIANISCHNIKOW, D. N., Weitere Beiträge zur Kenntnis der Keimungsvorgänge. Landw. Versuchsst. **46**:459–470. 1896.
30. ———, Eiweiszerfall und Atmung in ihren gegenseitigen Verhältnissen. Landw. Versuchsst. **52**:137–164. 1899.
31. ———, Über den Einfluss der Temperature auf die Energie des Eiweisszerfalls. Ber. Deutsch. Bot. Gessels. **18**:285–291. 1900.
32. SCHULZE, E., Über den Umsatz der Eiweissstoffe in der Pflanzen. Zeitschr. Physiol. Chem. **30**:241–312. 1900.
33. SCHULZE, E., STEIGER, E., and MAXWELL, W., Untersuchungen über die Chemische Zusammensetzung einiger Leguminosensamen. Landw. Versuchsst. **39**:269–326. 1891.
34. SPOEHR, H. A., and MCGEE, J. M., Studies in plant respiration and photosynthesis. Carnegie Inst. Washington Publ. **325**:1–98. 1923.
35. STARK, R. W., Environmental factors affecting the protein and the oil content of soy beans and the iodine number of soy bean oil. Jour. Amer. Soc. Argon. **16**:636–645. 1924.
36. THOMPSON, T. G., The total amino nitrogen in the seedlings of the Alaska pea. Jour. Amer. Chem. Soc. **37**:230–235. 1915.
37. WASNIEWSKY, S., Der Einflusz der Temperature, des Lichtes und der Ernährung mit Stickstoff und Mineralstoffen auf den Stoffwechsel in den Keimpflanzen des Weisens. Bull. Acad. Sci. Cracovie **1914**:615–686. 1914.
38. ZLATAROFF, As., Phytobiochemische Studien. Biochem. Zeitschr. **75**:200–210. 1916.

REVISION OF THE GENUS BEJARIA MUTIS

B. FEDTSCHENKO AND N. BASILEVSKAJA

Historical sketch

The first specimen of the genus *Bejaria* was found by MUTIS in 1761 in Colombia (New Granada), near Santa Fé de Bogota, on calcareous declivities (2800–3200 m.). MUTIS sent the specimen to LINNAEUS, and called it *Bejaria* as a compliment to his friend BEJAR, a professor of Cadiz. LINNAEUS, misreading *j* for *f*, published it under the erroneous name of *Befaria aestuans* in *Mantissa* 1771, p. 242, where it was faultily mentioned as native of Mexico. A little later MUTIS sent another specimen from the same place, and in LINNAEUS' *Supplementum* we find two species of *Befaria*, *B. aestuans* and *B. resinosa*, mentioned thus early as coming from Colombia. During a long time the new genus was quite unknown in Europe, and no herbarium possessed a specimen of it. There had reached Sweden nothing but a single description, and that of *B. aestuans*. That is the reason why RUIZ and PAVON, the Peruvian explorers, having found some representatives of *Bejaria* in Peru, described them as a new genus, *Acunna*, with two species, *A. oblonga* and *A. lanceolata*. The identity of *Acunna* with the genus *Bejaria*, however, was established beyond question by ZEA, pupil of MUTIS, and later by VENTENAT (Syst. Veg. flora Peruv.).

The unwarranted segregation of the genus *Acunna* having crept into literature, many authors have repeated it until the present day; this notwithstanding the fact that ZEA, CAVANILLE, and others had very promptly shown the error of RUIZ and PAVON. We prefer to use the real name, *Bejaria*, given by the first collector. This name might well have been spelled "*Beharia*," however, to accord with the Spanish pronunciation.

In 1800 VENTENAT (in Hort. Cels. N. et tab. 51) described a new species, *B. racemosa*, native of Florida and collected by MICHAUX. The collector intended to call it *B. paniculata*, because many of his specimens had a paniculate inflorescence; but since VENTENAT, indi-

cating such type of inflorescence as an abnormal deviation, published it under the name of *B. racemosa*, the later name of *B. paniculata* (Michx. Bor. Amer. 1803) must be taken as a synonym.

In 1809 the authors of *Nova Genera et Species*, HUMBOLDT and BONPLAND, published the description of four species brought all at one time from Colombia, Ecuador, and Peru. Then in 1837 HARTWEG found the first representatives in Mexico, *B. mexicana*, *B. laevis*, and *B. discolor*. This, however, did not prevent TURCZANINOW from describing a new genus, *Jurgensenia*, with one species, *J. mexicana*, which undoubtedly is *B. discolor*.

All these species of *Bejaria* are attractive shrubs or trees, often reaching the height of 8–10 m., with large scarlet or white flowers. *Bejaria* is called by horticulturists "the rose of the Andes," in allusion to its resemblance to "the rose of the Alps" (*Rhododendron*), a genus lacking in South America. The first attempts toward its cultivation were made late in the eighteenth century. These attempts evidently were highly successful, as is evidenced by the large lists of cultivated Bejarias given as early as 1850 in PAXTON and LINDLEY'S *Flower Garden*. We may add that their cultural handling is not especially difficult, although a damp atmosphere and free circulation of air in summer are no doubt essential.

Geographical distribution

The "rose of the Andes" is chiefly distributed in the Andes of South America, reaching the southern limit of 22° S.L. in the mountain region of Bolivia. Separate representatives are found also in North and Central America, however, one species in Cuba (Pinar del Rio), four in Mexico, and one in Florida and southeastern Georgia. The northern limit of the genus is found at 30° N.L. In South America the area of *Bejaria* is coextensive with the ridge of the Andes from Venezuela to Bolivia.[1] Three species only are found in British Guiana, at Mount Roraima. We cannot for a certainty deny the existence of one or more representatives of the genus in Guiana between the Andes of Venezuela and Mount Roraima, be-

[1] In *Index Kewensis* one species, *B. sprucei*, is erroneously mentioned as native of Brazil. Tarapoto, where *B. sprucei* is found, is on the eastern extension of the Andes of Peru, and *B. sprucei* is nowhere to be found in Brazil.

cause only a few investigators have visited this country; but we may mention here that there are a number of genera of the northern Andes (as regards South America) which have passed along the coastal Andes to Silla de Caracas, and yet do not extend southward over Bolivia; also which have reached Mount Roraima, but not southern Brazil.

The genus *Bejaria* is a typical representative of the alpine and sub-alpine vegetation of the Cordilleras. It frequently reaches considerable altitudes; thus for instance, in Bolivia *B. denticulata* is found at the upper limit of vegetation. The greatest number of South American species of *Bejaria* are distributed in Colombia, where eighteen of thirty-five species were found. Many of them are endemic. There is also a great diversity of forms and conditions of vegetation in this country. The most common range of distribution is the zone where the temperature is frequently 12°–14° C. during the day and 4°-6° C. at night. SIEVERS mentions a particular region in the Sierra Nevada in Colombia, at about 2800–3100 m., where *Bejaria* is found in great quantity, giving the character to the landscape. Here it appears as a small tree 3–4 m. high, growing alone or forming little groves. In the province of Socorra and Antioquia, certain species descend to 1500 m., while at the same time *B. aestuans* and *B. phyllireaefolia* are frequently met at the height of about 4000 m. From Colombia the species of *Bejaria* are penetrating into the Andes of Venezuela, where they are found in the dry woods of Sierra Merida and Silla de Caracas, often at the upper limit of trees. *B. glauca* was collected by FUNCK in the environs of Caracas at 1500 m., where it was growing in dry sunny and sandy places, together with *Gaultheria coccinea* and *G. odorata;* they are the most typical plants of the subalpine zone. In the woods in deep shade it often reaches 10 m. in height. The limit of its distribution is at 2000 m., where it gives place to another species, *B. ledifolia*, and often *B. grandiflora*, which here represent the alpine zone of vegetation with *Gaylussacia buxifolia*, some *Vaccinium* sp., and others. On the contrary, *B. ledifolia* grows only at an altitude of 1900 m. and upward. On the southern declivities of Silla de Caracas there are many thick groves formed by *B. ledifolia*. We have mentioned already that in the eastern part of Venezuela *Bejaria* is absent and

appears only in British Guiana, with three species on Mount Roraima at 2400 m. These species are here endemic, and represent a closely allied group. To the southwest of Colombia the genus is distributed in Ecuador, Peru, and Bolivia. In Ecuador five species are present in the Valley of Loja, in Paramo de Saraguru, at about 2000 m. Here there is a warmer climate with average temperature of about 15°–18° C. *Bejaria* grows also in Quito where the climate is more dry and cold. Two of the Ecuadorean species are endemic; the other three occur also in Colombia and Venezuela. Out of eight species growing in Peru, three only are common in Colombia and Ecuador; the other five are endemic on the eastern declivities of the west Cordillera, in the mountain basin of Caxamarca at 2700 m., in the middle Cordillera, Chachapoyas, Huanaco, Tarapoto. The climate here is drier and colder. Finally, in Bolivia "the rose of the Andes" reaches its southern limit. Here already *B. glauca* is met at the same altitude of 1500–2000 m., between the shrubs of Tres Cruces and Yungas; *B. denticulata*, a second Colombian species, is found in the alpine zone of Mount Viscahal. There are three species endemic in Bolivia, dwelling in Yungas and upon the eastern declivities of the Cordilleras. The Colombian-Venezuelan Andes, however, is the center of *Bejaria* development in the present day, and from there it is penetrating into the neighboring mountain regions of South America.

In Central America the distribution of *Bejaria* is of such character as to suggest merely a survival from the past. The species found here are more ancient and but little differentiated. Four of them are found in Mexico: in the province of Oaxaca, near Villa Tanatze, in the middle Mexican province of Zacatecas, Balanos, and at Sierra Madre in the province of Durango. All of these habitats are in the mountain region of Mexico, among the southern Cordilleras. In the central part between Colombia and Oaxaca species of *Bejaria* are absent. In the Antilles one species is found in the western part of Cuba (Pinar del Rio). Probably it originates from Central America, whence it came in the Tertiary time when there was a land bridge between Central America and the West Indian islands. A permanent isolation and differentiation brought about subsequent endemism of this species.

In North America one species[2] is distributed in Florida and South Georgia. It is *B. racemosa* Vent, a relict and primitive type, a low shrub, with green, large leaf-blades and long, large racemes or panicles much exceeding the leaves. It is much more like *Rhododendron canadensis* than a species of *Bejaria* of South America. *B. racemosa* is found growing in dry pine barrens throughout the Florida peninsula to southeastern Georgia.[3] The most northern situation is on Cumberland Island, where it is a shrub 1.5–2 m. high, growing in dry sandy soils. In gardens around Charleston (South Carolina), where it frequently is introduced, it never flourishes.

It already has been mentioned that the name of "the rose of the Andes" was given to *Bejaria* because of its external similarity to *Rhododendron*. As a matter of fact, its large bright flowers, disposed in a dense inflorescence and often with a pattern in the throat, also its coriaceous, sometimes large, leaves call to mind many species of *Rhododendron*. In the following revision of relationships we shall have occasion to speak about a close alliance between the two so-called "roses" of Ericaceae; here, however, we shall allude only to the resemblance in their geographical distributions. *Rhododendron* is distributed in North America, chiefly in northern, northeastern, and eastern parts of the continent. Many species are frequent in the Rocky Mountains, reaching southward to the boundary of Mexico, and passing over into California. Some species are found also in Florida and Georgia, but in Mexico and farther on not one species is found. Here the "rose of the Andes" appears and takes the place of the alpine one.

Origin and relationships

All that has been said thus far about the geographical distribution of *Bejaria* shows that the ancient distributional area was much broader than it is at the present time. The genus was distributed

[2] A second North American species was described by GANDOGER in Bull. Soc. Bot. France. **65**: IV série. 1918; it is somewhat doubtful, however.

[3] Central peninsular Florida is a lake region. There are five well marked areas, the flora of each being different: high pine land, low pine land, shrub, bay heads, and hammocks. *Bejaria racemosa*, together with *Podostigma pedicellata*, *Rhexia ciliosa*, *R. serrulata*, *Aristida stricta*, and *Andropogon floridanus*, is peculiar to the formation of low pine land, where *Pinus serotina* and *P. caribaea* are the prevailing trees.

throughout North America. Probably *B. racemosa* occurred in the Appalachian mountains; originally developed as a mountain form, it spread during the glacial period down to the coastal plain. After the ice sheet had moved off the plateau, which suffered glaciation, many of the old plateau forms returned, but *B. racemosa* did not; it remained in the plain and migrated southward, where it found favorable conditions, while in other places which marked its distribution in the great Miocene forest it had become extinct because of unfavorable conditions. In Florida we find a veritable colony of northern plants. All the territory above the great terminal moraine was a country influenced by the glacial cold, where tundra conditions prevailed. All the country south of it, protected by the Alleghany Mountains, was covered by a forest composed of those species that had existed in this region and also in the far north prior to the advent of the last glacial epoch. Here is to be found a mesophytic association of plants that is or was abundant farther north. Among the plants of this association are *Bejaria racemosa, Elliottia racemosa*, and some *Rhododendron* species. We have thus traced the development of *Bejaria* in eastern North America during the glacial period, but previous to it the *Bejaria* species were distributed in Mexico and South America.

Notwithstanding the fact that the main proportion of species is found in South America, while only a few occur in North and Central America, we cannot indicate the Colombian-Venezuelan Andes as the geographic center of origin of *Bejaria* in early times. This genus originated undoubtedly from North America, if we may adopt a hypothesis formulated in view of the relationship of *Bejaria* and North American Ericaceae. As to its taxonomic position among the Ericaceae, *Bejaria* is here placed among the Rhododendroideae-Ledeae, with other Ericaceae having distinct petals. The group here mentioned, *Bejaria* excepted, embraces four genera, one of which is a native of Japan, two of North America, while one is widely distributed in North America and in Europe. Among the genera of the group three have an exceptional number of perianth lobes: *Elliottia* has four petals and eight stamens, *Tripetaleia* three petals and six stamens, and *Bejaria* 6–8 petals and 12–16 stamens. Only two genera have five petals and ten stamens, the number usual for a

great proportion of Ericaceae. These are (1) *Ledum*, a widely distributed circumpolar genus with five species, occurring throughout the northern and western part of North America (Rocky Mountains) and spreading down to California, and (2) a monotypic genus *Cladothamnus*, growing only in the western states from Alaska to Oregon.

Aside from these near relatives allied to *Bejaria* in the distinct petals and the form of the embryo, there is manifest a close alliance with the group Rhododendroideae, or more particularly with the Rhododendreae and their chief representative, the polymorphic genus *Rhododendron*. The reference of *Rhododendron* together with the other genera *Menziesia* and *Tsusiophyllum* to the group Rhododendreae is based by ENGLER on the petals, which are slightly united, and on a cylindric form to the embryo. But some species of *Rhododendron*, for instance *R.* (*Rhodora*) *canadensis*, have a short corolla tube and the petals nearly distinct. The form of the seeds is very similar to that in *Bejaria* and closely allied genera. But a greater resemblance exists between the two groups, namely, the uniting of the pollen with long threads into a pollen mass. We succeeded in establishing that in the group of Ledeae all the genera, *Ledum* excepted, have such a pollen mass, which, according to ENGLER, is usual for Rhododendreae. On the other hand, *Menziesia*, belonging to Rhododendreae, has the pollen without threads.

The nearest relatives of our genus, however, which have originated in one genetic branch of Ericaceae coming from Asia to eastern and southern America, are evidently two genera. One is *Elliottia*, in the group Ledeae, distributed in the southeastern part of the continent to the northern limit of *B. racemosa* (eastern Georgia and adjacent South Carolina). This monotypic genus is closely allied to *Bejaria*, and is very similar to *B. racemosa* in the matter of stature, in the long and broad racemose or paniculate inflorescence, in the leaves with a terminal gland on the midrib, and in a broad short calyx. The other is *Rhododendron* in the group Rhododendreae, the affinity of which was already mentioned. Probably very near also is *Ledothamnus*, placed by ENGLER in the neighboring group Rhododendroideae-Phyllodoceae. This genus is monotypic and endemic in British Guiana. The number of petals, quite distinct, is not con-

stant, but averages 5 or 6, the stamens being always twice the number of the petals. We have no specimens of this genus in the herbaria of Russia and cannot decide finally for *Ledothamnus* its degree of affinity. ENGLER distinguishes the group Phyllodoceae from Rhododendreae by the form of the seeds, these not at all winged but thick and triangulate, and by the absence of union among the pollen grains. We could not decide whether this is right for *Ledothamnus*, but for the closely related genus *Leiophyllum* it is quite exact.

Thus we see that all the relatives of *Bejaria* are distributed in North America and partly in northern Asia, and it seems to be clear that the genus originates not from South America but from North America.

Unfortunately, in the realm of phytopaleontology we have today no idea of the recent history of the genus. From the group Rhododendroideae the genus *Dendrium* (segregated from *Ledum*) is found together with *Leucothoe* and *Gaylussacia* in the Pleistocene of North America (New Jersey). In the lower Tertiary some leaves are found and described under the name *Tripetaleia almquistii*, but not a single fragment of *Bejaria* or of closely allied genera have been found in North America.

During the Tertiary, Florida and the portion of North America which now comprises the Atlantic and Gulf Coast plains were beneath the Atlantic Ocean. The ancestors of *Bejaria* and of the allied genera *Elliottia* and *Rhododendron* were growing at that time throughout North America and probably northern Asia, a land connection being present during that time between the two continents. The North American Tertiary flora covered the entire land areas of the continent. The climate of the Eocene and Miocene periods was milder than at present, and over much of North America was somewhat subtropical in character. Also, the flora of these periods was fairly uniform in character from the Atlantic to the Pacific oceans, and from the American Mediterranean northward and into the arctic regions, and this flora, especially in the southern part of the Tertiary American continent, was of subtropical character; that is to say, in the great Tertiary forests the ancestor of our genus was growing. It was a mesophytic shrub with large evergreen leaves (bright on both sides), with a long and lax racemose (or paniculate) inflo-

rescence which exceeded the leaves and was covered with fine tomentum; flowers with five petals quite separate, as also the sepals; stamens twice the number of the petals and also free. The uniformity of flora and of climatic conditions did not contribute to differentiation, and traces of the mesophytic ancestor we find at present in *B. racemosa*, a survivor from the great Tertiary forest. The migration of *Bejaria* into Mexico began in a former epoch, in the Eocene, or Paleocene, when many northern plants reached Central America. When the representatives of *Bejaria* made their appearance for the first time in Mexico they met there very different conditions and also a foreign flora. During Tertiary times the climate of Mexico was much drier than that of North America. The differentiations of the immigrants from the north began in response to desert conditions, because the desert type of vegetation here was replacing the forest of North America. At the present time four species are growing here, belonging to two genetic branches. They are direct descendants of the ancestral type; the leaves are distinctly different and there are considerable differences in size, habit, infloresence, and pubescence, characters partly modified by the environment. Already we see here the species differentiated into two groups; in the first group the pubescence of the branches, peduncles, pedicels, and leaf blades is deciduous or absent, while in the second group it is persistent and becoming glandulous. From Mexico the species of *Bejaria* penetrated into the Antilles, probably in the Eocene, when a land bridge connected Mexico and the West Indian islands. At the end of the Eocene and during the Oligocene and Miocene, this connection was severed. With the depression of the islands in subsequent periods, the West Indian land mass was broken up into physiographically distinct regions, and the present differentiation of the flora began at that time. This is the cause of a large number of endemic types in the West Indian flora. The unique species of our genus, *B. cubensis*, growing in Cuba, is an example of such an isolated and therefore very much changed form.

In late Miocene a land connection established itself between the two American continents, and the Tertiary flora of North and Central America penetrated to the southern continent. At this very time the formation of the Cordilleras was completed, and *Bejaria*

together with other tropical plants became distributed in the mountain region of the western Andes. Evidently here the most favorable climatic and edaphic conditions were found. This is shown by the development of *Bejaria* species; in South America there are growing thirty-six out of the forty-two species of the genus. The South American species can be regarded as direct descendants of those of Central America which have been evolved in response to mountain conditions. The diminution of the leaf blades and inflorescence (racemes transforming into corymbs or umbelliform clusters) is clearly an adaptation to the habitat.

The relationships among these species cannot be taken up in detail in a final way, because of the small number of specimens in Russian herbaria. However, it seems desirable here to sketch the lines of evolutionary development, at least so far as our material, containing many authentic specimens, will permit. It does not follow that the results represent more than the probable relationships. It is believed, however, that this attempt to place the species into natural evolutionary groups will be of service.

These species of *Bejaria* are very constant in the structure and development of the flowers and fruits, although the best criteria for the recognition of sections are wanting. The differences in the type of inflorescence and pubescence, however, are of such importance that they may be used as a basis for the sections of the genus. Thus the presence or lack of glandular hairs, the persistence or the complete disappearance of the peduncles and pedicels, and the disposition of the flowers in racemes, corymbs, or panicles are recognized as sectional characters.

The present species of *Bejaria* can be arranged in four sections; their distinguishing characteristics and their probable relationships are indicated in key form as follows:

1. Inflorescence always a long, lax, terminal, solitary panicle or raceme, much exceeding the leaves; leaves bright green on both sides.....I. Racemosae
2. Inflorescence umbelliform or a shortened raceme, panicle or corymb with congested flowers, rarely solitary and as a rule scarcely exceeding the leaves; leaf blades mostly glaucous beneath
   A. Peduncles and pedicels glabrous or covered with fine deciduous pubescence.....II. Laeves

B. Peduncles and pedicels covered with persistent tomentum and spreading glandular hairs.....III. Glandulosae

C. Peduncles and pedicels covered with persistent tomentum and often spreading but not glandular hairs

IV. Eglandulosae

a. Inflorescence corymbose.....§ *Corymbosae*

b. Inflorescence racemose or panicled.....§§ *Racemosae*

This arrangement is based on the assumption that the genus *Bejaria* was derived from an ancestor resembling *Elliottia* and *Rhododendron*, in which a long, racemose inflorescence and a sparse and not glandular pubescence were present. Probably the leaf blades also were pubescent, because certain species yet exhibit a strong tendency to retain the tomentum, while others have an equally strong tendency to drop it.

It has been shown that the contact of *Bejaria* with the genus most closely related to it, *Elliottia*, apparently is best represented by *B. racemosa*. This does not necessitate the assumption that the other sections have arisen through this one. Such a hypothesis would lead to the conclusion that the character of panicled inflorescence and that of the spreading pubescence of the peduncles were once developed and then lost in some groups of species. While this is possible, it seems improbable. More logical is the assumption that the *Bejaria* stalk was developed from an ancestor close to *Elliottia*. The development first concerned itself with the modification in the number of the parts of the perianth and the valves of the fruit, also in quantity of seeds. It was perhaps from such a group that *B. racemosa* was derived, probably together with some other species which vanished in course of time.

The hypothetical group already mentioned gave rise somewhat farther up to the *Laeves*. It seems true that this section is more primitive than either of the two remaining, in view of the fact that each of them exhibits some characters not possessed by *Laeves*, and indicative in each case of a higher order of development. We see here the abbreviation of the peduncle which is typical also in the succeeding groups, but in *Laeves* it is followed mostly by a protraction of pedicels and the complete disappearance of the tomentum. Leaf blades are very broad in *Laeves* (or, if narrow, not so thick and coriaceous in texture) and quite glabrous, but sometimes glaucous beneath.

In order to reach the remaining two groups it is necessary to leave the line which culminates in the most highly modified species of *Laeves*, and pick up a new evolutionary thread somewhere apart from the basis of *Laeves*. This is necessitated by the appearance of a very important character, namely the dense and persistent tomentum of the peduncle and pedicels. This tomentum is often followed with spreading hairs, glandular in the *Glandulosae*. The sections *Glandulosae* and *Eglandulosae* are closely allied, and this is a case of parallel variation in two groups of species not widely separated phylogenetically. The species of the *Eglandulosae* may be divided into two groups because of two different types of inflorescence, *Racemosae* and *Corymbosae*, the first with the racemose, the second with the corymbose, type. Both groups are so much alike that there can be no doubt as to their close phylogenetic origin. In the *Corymbosae*, however, the abbreviation of the inflorescence is carried to a high type, and is followed by the enlargement of the flower and other characters of high specialization not reached by the *Racemosae*.

Key to species of Bejaria

I. RACEMOSAE.—Flowers disposed in a solitary raceme or panicle much exceeding the large green leaves; one species in North America ..... 1. *B. racemosa*

II. LAEVES.—Flowers disposed mostly in a corymb or shortened raceme; pedicels glabrous

1. Flower stalks protracted, much longer than the flowers; peduncle short, inflorescence large
   a. Leaf blades broad, ovate or elliptic, obtuse
      1. Branches covered with spreading hairs ... 2. *B. subsessilis*
      2. Branches glabrous ..... 3. *B. drymifolia*
   b. Leaf blades narrow, lanceolate
      1. Leaf blades green beneath ..... 4. *B. laevis*
      2. Leaf blades glaucous beneath ..... 5. *B. ghiesbreghtiana*
2. Flower stalks not protracted, scarcely or no longer than flowers, peduncle very short; inflorescence narrow, corymbose 6. *B. glauca*

III. GLANDULOSAE.—Flowers disposed in 1–5 racemes, panicles, or corymbs; peduncle and pedicels covered with glandular hairs

1. Flowers in terminal, solitary, lax racemes; leaves nearly linear, strongly revolute; Cuba.....7. *B. cubensis*
2. Flowers in terminal, sometimes axillary racemes or panicles with a short peduncle
   a. Glandular hairs deciduous, flower stalks becoming glabrous; leaf blades broad, 3.5–6 cm.; inflorescence many-flowered, broad.....8. *B. discolor*
   b. Glandular hairs persistent, but the gland-top deciduous; flower stalks always pubescent: leaf blades small, 1.5–2.5 cm.; inflorescence a few-flowered corymb.....9. *B. mexicana*
   c. Glandular hairs persistent
      1. Inflorescence large, panicled, or the flowers disposed in 1–5 racemes; leaf blades always pubescent beneath
         a. Inflorescence terminal and axillary; leaf blades dark beneath.....10. *B. sprucei*
         b. Inflorescence terminal; leaf blades glaucous beneath (except in *B. denticulata*)
            Leaf blades glandular-pubescent, green or scarcely glaucous beneath
               Leaf blades minutely toothed, branches covered with black pubescence.....11. *B. denticulata*
               Leaf blades entire, branches covered with ferruginous pubescence.....12. *B. guianensis*
            Leaf blades tomentose
               Leaf blades pubescent beneath only; petals seven 13. *B. antioquiae*
               Leaf blades pubescent on both sides; petals six 14. *B. hispida*
      2. Flowers disposed in racemes much exceeding the leaves; leaf blades very pubescent on both sides when young, then glabrous except as to glandular hairs of midrib beneath
         Petals six; calyx lobes united about the middle 15. *B. lindeniana*
         Petals seven; calyx lobes distinct nearly to base 16. *B. aestuans*
3. Flowers disposed in corymbose or umbellate inflorescence,

this scarcely exceeding the leaves; leaf blades glabrous, small, with glandular hairs on midrib

Leaf blades almost flat, with slightly revolute margin

Petals seven; flowers pink.....17. *B. densa*

Petals 6–8; flowers pink or purple

Calyx and corolla glabrous.....18. *B. imthurnii*

Calyx and corolla viscid.....19. *B. resinosa*

Leaf blades very revolute, with glandular hairs

20. *B. ledifolia*

IV. EGLANDULOSAE.—Peduncle and pedicels tomentose, without glandular hairs

Racemosae.—Flowers disposed in racemes or panicles

1. Leaf blades pubescent, pubescence persistent; flower stalks much longer than calyx

a. Peduncles tomentose

1. Branches glabrous; leaf blades acute; petals lanceolate

21. *B. pallens*

2. Branches pubescent; leaf blades obtuse; petals obovate

22. *B. mathewsii*

b. Peduncles covered with spreading hairs

1. Flowers in racemes, leaf blades minutely toothed

23. *B. subserrata*

2. Flowers in panicles, leaf blades entire...24. *B. boliviensis*

2. Leaf blades pubescent when young, then mostly glabrous; flower stalks twice length of calyx.....25. *B. grandiflora*

3. Leaf blades always glabrous; flower stalks 3–5 times length of calyx

a. Leaf blades broad, obtuse; flower stalk reaching scarcely 1 cm.....26. *B. parviflora*

b. Leaf blades narrow, acute; flowers longer than 2 cm.

27. *B. decora*

Corymbosae.—Flowers in corymbs

1. Leaf blades pubescent, leaves with revolute margins

a. Leaf blades covered with spreading hairs....28. *B. congesta*

b. Leaf blades tomentose

1. Pubescence of the branches, leaf blades, and flower stalks ferruginous.....29. *B. lehmanniana*

2. Pubescence of the branches, leaf blades, and flower stalks gray.....30. *B. grisea*

2. Leaf blades dense-pubescent when young, then almost glabrous

a. Leaf blades about 2.5 cm. long or less, revolute 31. *B. myrtifolia*

b. Leaf blades about 2.5 cm. and longer, flat 32. *B. caxamarconsis*

3. Leaf blades glabrous

a. Peduncle short, flowers disposed in many-flowered corymb, about 2 cm. in length.....33. *B. coarctata*

b. Peduncle long, corymb large, many-flowered, flowers less than 2 cm. long.....34. *B. phillyriaefolia*

c. Peduncle very short, flowers disposed in a few-flowered, solitary, subcorymbose raceme, about 4 cm. in length

1. Bracts shorter than flower stalks.....35. *B. popayana*

2. Bracts equal to flower stalks.....36. *B. corymbosa*

I. RACEMOSAE

1. B. RACEMOSA Vent. Descr. pl. Cels. pl. 51. 1800; SMALL, North Amer. Fl. **29**:36; DC. Prodr. **7**:731.—*B. paniculata* Michx. Fl. Bor. Amer. **1**:280. pl. 26. 1803.

North America: Florida, dry pine barrens near Jacksonville, June 16, 1894; A. CURTISS 922! and 1728; vicinity of Eustis, Lake County, GEO. V. NASH 803, May 16, 1894; Florida (without locality), RICHARD and COOPER; Cumberland Island, southeastern Georgia; South Carolina; in herb. Gasstromic (Stockholm).

II. LAEVES

2. B. SUBSESSILIS Benth. Plantae Hartwegianae 143; JAMESON, Synops. Pl. Aequat. **2**:198; Walp. Rep. **6**:420.

Ecuador: Quito, at Mount Loja, JAMESON, HARTWEG 797.

3. B. DRYMIFOLIA Linden, ex Hérincq. Revue Hortic. 3:185. 1850.

Colombia (New Granada): In the province of Pampelona, LINDEN 1456. 1847; KARSTEN, Bogota; Venezuela, Silla de Caracas, LINDEN 12, 1842.

The specimens from Silla de Caracas and Bogota are not quite identical with those of Pampelona. They have the inflorescence much shorter and the flower pink.

4. B. LAEVIS Benth. Pl. Hartweg. 65; Walp. Rep. 2:730; HEMSLEY, Biolog. Centr. Amer. 2:282. 1881–1882; SMALL, North Amer. Fl. 29:1914.—*B. glabra* Mart. et Galeotti, Bull. Acad. Brux. 1842.

South Mexico: Talea to Totontepec, HARTWEG 478; Eastern Cordillera of Oaxaca at 5000 ft., GALEOTTI 1811.

5. B. GHIESBREGHTIANA (Planchon) nob.—Fruticosa: rami ramulique glabri, vel sparse hispidi: folia lanceolata 6–8 cm. longa, 1.5–1.8 cm. lata, utrinque attenuata, acuta, breviter petiolata, supra minute adpresse tomentosa, vel glabra, subtus glauca semper glabra, integerrima, petiolis glabris: inflorecentia racemosa, subcorymbosa, racemi solitarii, parviflori, apice ramulorum dispositi; pedunculus pedicellique subglabri, juveniles sparse adpresse tomentosi, deinde glabri; pedicelli tenues 3.5 cm. longi, bracteis parvis, deciduis: calyx campanulatus, glaberrimus, lobis 7, ovatis, obtusis, mucronatis margine ciliatis: petala 7 obovata basi attenuata, 2–2.5 cm. longa, 8–9 mm. lata, ad faucem pubescentia: stamina 14, petalis aequilonga, basi dilatata, pilosa: stylus supra calycem incrassatus (in sicco 1.5 mm. latus) stigmate magno.

Mexico: Province of Oaxaca, M. GHIESBREGHT, 1842–43. Allied to *B. laevis*, but differs in glaucous leaf blades and larger flowers.

6. B. GLAUCA Humb. et Bonpl. Aequinox. 2:118. tab.; H.B.K. Nov. Gen. Amer. 3:227; DC. Prodr. 7:731; MORREN, Ann. Soc. Hort. de Gand 1:61; PAXTON and LINDL. Flower Garden 1:84.

Venezuela: Mount Silla de Caracas, H.B.K.; without locality, OTTO 696; Tovar, FENDLER 743; Colombia or Ecuador, LEHMANN without locality 4964; CALBEREYER 867; Bolivia, bush region of Tres Cruces, north of Santa Cruz, about 1560 m. alt., HERZOG 1611.—A widely distributed species.

III. GLANDULOSAE

7. B. CUBENSIS Griseb. Cat. Pl. Cub. 52; SMALL, North Amer. Fl. 29:35. 1914.

Cuba: Pinar del Rio, western Cuba, WRIGHT 2200.

It is difficult to determine the exact position of this species in the phylogenetic scheme of the species of *Bejaria*. This is due to its scarcity and its local distribution. We have placed it among the Glandulosae because of the glandular hairs covering it. Here it must be placed near *B. mexicana* and *B. discolor*, although very much modified and with highly specialized characters.

But the long, always solitary raceme is very similar to that of *B. racemosa*. We assume, however, that the raceme of *B. cubensis* is a secondary formation, evolved in response to a long isolation and to original conditions. This assumption is based on a high differentiation of the raceme of *B. cubensis*, in comparison with that of *B. racemosa*.

8. B. DISCOLOR Benth. Pl. Hartweg. 65; Walp. Rep. 2:730; Hemsl. Biolog. Centr. Amer. 2:282; SMALL, North Amer. Fl. 29:36. 1914; *B. paniculata* Gal. in Herb.; *B. floribunda* Mart. et Gal. in Bull. Acad. Brux. 9:18; *Jurgensenia mexicana* Turcz. in Bull. Soc. Nat. Mosc. 20:151.

South Mexico: Talea, HARTWEG 479; mountains of the eastern Cordillera of Oaxaca, near Villa Alta and Tanatze, GALEOTTI 1812, 182; Sierra San Pedro Nolasco, JURGENSEN 391, 562; Sille, W. W. SAUNDERS (in herb. Kew Gard.).

This species represents an intermediate stage between Laeves and Glandulosae, most nearly approaching the species of Laeves by the ample foliage, the protraction of the pedicels, and the deciduous pubescence. But the glandular hairs are fairly well developed and deciduous only at the time of fructification, and the calyx and corolla are more pubescent and sometimes viscid as is usual for Glandulosae. The specimen of GALEOTTI (1812) described under the name of *B. floribunda* Mart. has a very long and broad inflorescence, and the young leaves are quite pubescent.

9. B. MEXICANA Benth. Pl. Hartweg. 15. 1839; HEMSL., Biolog. Centr. Amer. 2:282. 1881–82; Seem. Bot. Voy. "Herald" 317; SMALL, North Amer. Fl. 29:36. 1914.

North Mexico: Sierra Madre, on the road from Mazatlan to Durango, SEEMAN 2130; South Mexico: Balanos, Zacatecas, HARTWEG 69.

10. B. SPRUCEI Meissn. in Mart. Fl. Brasil. 7:171.

Eastern Peru, near Tarapoto, SPRUCE 3994 (1855–6).

11. B. DENTICULATA Remy, Ann. Sc. Nat. III. 8:236. 1847; WEDDEL Chloris Andina 2:182. 1857; WALPERS, Annals 1:482.

Bolivia: In the province of Yungas at the upper limit of vegetation; on Mount Viscachal, d'Orbigny; Colombia (New Granada), in the province of Socorra, LINDEN 766; FUNCK and SCHLIM 1332.

12. B. GUIANESIS Klotzsch in R. Schomb. Reisen in Brit. Guiana 3:1088; N. E. BROWN in Trans. Linn. Soc. 6:46; OLIVER in Trans. Linn. Soc. 2:276. 1887; APPUN, Unter den Tropen 2:232, 287, 292.

We know this species only by the short description given in N. E. BROWN'S publication (report on two botanical collections from Mount Roraima in

British Guiana), where it is said to be allied to *B. imthurnii*. It is only with doubt that we determine its position in the scheme of *Bejaria*, although its membership among the Glandulosae is evident; Brit. Guiana: Upper slopes and ledge of Mount Roraima, Shomburgk 1041; McConnell and Quelsh 40.

13. **B. antioquiae,** sp. n.—Frutex, ramis ramulisque dense tomentosis pilis glanduliferis vestitis: folia breviter sed distincte petiolata, coriacea, rigida, elliptico-oblonga, 4–6 cm. longa, 1.5–2 cm. lata, minute ciliato-denticulata supra glabra et lucida, subtus albo fulvoque pubescentia, glauca, nervo medio glanduloso-ciliato, supra sulcato, subtus prominulo: petioli hispidi: racemi fasciculati 1–4, terminales, densi et multiflori, 7–9 cm. longi, pedicellique ferrugineo-tomentosi et glanduloso-hirti: pedicelli elongati 2–5 cm. longi, bracteis oblongis, pedicellis duplo brevioribus, margine glanduloso ciliatis: calyx campanulatus, 7-lobatus, puberulus, lobis ovatis, obtusis, usque ad medium connatis, biseriatis, margine ciliatis: petala 7 oblonga, obtusa, minute pubescentia, 2 cm. longa: stamina 14, basi dilatata, pilosa, corollae subaequilonga: stylus longe exsertus.

Colombia: Antioquia, inter Yolombo et Cauca, 1500–2000 m., September, 1884, Lehmann 212.

Allied to *B. imthurnii* N. Brown, from which it differs in having its leaves pubescent beneath, toothed and more elongated, and in having its petals finely pubescent.

14. B. hispida Poepp. et Endl. Nova Gen. 1:24; DC. Prodr. 7:731.

Eastern Peru: In the province Huanaco, near Acomajo.

15. B. Lindeniana Hérincq. Rev. Hort. 3:183. 1850; *B. coarctata* Bot. Mag. 5:pl. 4433 (not *B. coarctata* H.B.K.).

Venezuela: from Silla de Caracas to Merida, 1843; Linden 387, Merida; Moritz 365, 1844–45.

The species published in Bot. Mag. (pl. 4433) is totally different from what is described by Humboldt and Bonpland under the same name. This error was pointed out by Hérincq, who called it *B. lindeniana*, in compliment to Linden, the horticulturist and collector. The discussion of this species showed the great difference between *B. coarctata* H.B.K. and that of Bot. Mag., a difference necessitating their placement in different sections.

16. B. aestuans Mut. ex Linn. Mant. 242, suppl. 247; Sp. Pl. 2:847; H.B.K. Nov. Gen. Am. 3:229; Humb. et Bonpl. Pl. aequi-

nox., 120; DC. Prodr. 7:731; Vent., Choix n. 52 in adn.; JAMESON Synops. pl. aequat. 197; VAN HOUTTE, Fl. des Serres 4:3288.—*B. oblonga* Pers. Ench. 2; *Acunna oblonga* Ruiz et Pav. Fl. per. syst. 123.

Colombia (New Granada): Santa Fé de Bogota, near Gonzanama, Mutis; from the type locality, FUNCK and SCHLIM 1604; Venezuela, FUNCK and SCHLIM 874; Merida; Ecuador; Quito, Mount Loja, JAMESON.

17. B. DENSA Planch. ex Hérincq, Rev. Hort. 4:185; *B. microphylla* Planch. ex Paxt. et Lindl. Flower Gard. 1:86; *B. albiflora* Linden in Hb. Vindobon.

Colombia (New Granada): Province of Pamplona, SCHLIM 1721; Chapo, 2400 m., LINDEN 1351!.

18. B. IMTHURNII N. Brown. Trans. Linn. Soc. 7:46; *Befaria* aff. *resinosae* Mutis, OLIVER in Trans. Linn. Soc. Bot. 2:278. 1887.

British Guiana: Summit of Mount Roraima, 8600 ft., THURN 310; MCCONNELL and QUELSH 94, 146.

19. *B. resinosa* Mutis, Ic. Am. ex Linn. Suppl. 246; DC. Prodr. 2:731; Vent. Choix t. 52; PERSOON, Synops. 3:1807; *Acunna lanceolata* Ruiz et Pav. Syst. Fl. Per. 123; *B. resinosa, B. lanceolata* G. Don Gen. Syst. 3:849.

Colombia: Santa Fé de Bogota, MUTIS. Santa Marta, H. SMITH 1406; Peru: on the high hills of Rodos Pillao and Huassa.

20. B. LEDIFOLIA Humb. et Bonpl. Pl. Aequinox. 2:124; H.B.K. Nova Gen. Am. 3:229; DC. Prodr. 2:731; VAN HOUTTE Fl. de Grochshor. 3:t. 3.

Venezuela: Silla de Caracas, LINDEN 128!; FUNCK 313; Colombia: MORITZ 365.

IV. EGLANDULOSAE

RACEMOSAE

21. B. PALLENS Remy in Ann. Sci. Nat. 8: 229. 1847; Walpers Annals 1:842.

Bolivia: In province Yungas on the way from Chilca to Chulmani (d'Orbigny), ESPIRITO SANTO BANG 4167.

22. B. MATHEWSII Field, Bot. Mag. t. 4981.

Peru: Province Jaulia, MATHEWS 1424!; province Chachapoyas, MATHEWS 1426.

23. **B. subserrata,** sp. n.—Frutex: rami minute tomentosi, ramulis hispidis: folia alterna, coriacea, rigida, oblonga, 3 cm. longa et 1–2 lata, apice obtusa vel acuta, basi in petiolum brevem angustata, supra lucida et glabra, subtus glauca albo-fulvoque pubescentia, margine denticulato-ciliata, nervo medio supra sulcato, subtus prominulo, adpresse tomentoso: inflorescentia racemosa, subcorymbosa, racemis 2 apice ramulorum dispositis: pedunculus pedicellique ferrugineo-tomentosi, pilis longis et glandulosis patenter vestiti: pedicelli tenues 2.5–3 cm. longi, bracteis caducis: calyx campanulatus, dense pubescens, 7-lobatus, lobis late ovatis, obtusis: petala 7, oblongo cuneata, apice rotundata, pubescentia: stamina 14 libera, basi pilosa, dilatata et petalis 2 cm. longis vix longiora: stylus exsertus, stigmate magno.

Venezuela: Without precise locality, FUNCK and SCHLIM 1331.

Allied to *B. denticulata*, which differs in its panicled inflorescence and in absence of glandular hairs on the pedicels and peduncles; from *B. caxamarcensis* it differs in its minutely toothed leaves and in the dimension of the flowers.

24. **B. boliviensis**, sp. n.—Frutex: rami glabri vel pulverulenti, ramulis hispidis: folia alterna, coriacea, rigida, oblonga, 3–4 cm. longa et 1.2–1.8 cm. lata, basi angustata, apice obtusa vel acuta, saepe obtuse mucronata, petiolata, supra lucida et glabra, nervo medio basi tomentosa, subtus glauca albo fulveque tomentosa, nervo medio setoso; petiolis hispidis: inflorescentia dense paniculata ramosa, pedunculis pedicellisque patenter ferrugineo-pilosis, pilis longis, eglandulosis: pedicelli ca. 2–2.5 cm. longi, crassi; bracteis foliis non dissimilibus hispidissimis, deciduis, margine denticulatis, quam pedicellis triplo brevioribus: calyx campanulatus, 7-lobatus, pubescens, lobis ovatis, obtusis: petala 7 oblonga, obtusa, juvenilia pubescentia deinde glabra, 1–1.3 cm. longa: stamina 14 (-15) usque ad medium pubescentia, basi dilatata, brevissime inter se connata: stylus crassus exsertus.

Bolivia: "From 1500 to 2000 miles in the interior, lat. 15–18° south," BRIDGES 177; MANDON 563!.

Allied to *B. subserrata*, but differs in its inflorescence and entire leaves.

25. B. GRANDIFLORA H.B.K. Nova Gen. **3**:228; Humb. et Bonpl. Pl. Aequinox. **2**:122; DC. Prodr. 2: 731; JAMESON Synops. pl. Aequator. **2**:197. 1865.

Ecuador: Quito; in the province of Loja, Paramo de Saraguru, Humb. and Bonpl.; JAMESON; HARTWEG 716: Venezuela, without locality, FUNCK and SCHLIM (1847) 1329! Colombia: Cauca, Popayan (1884) Lehmann 220.

26. B. PARVIFLORA Benth. Pl. Hartweg. 143; Walp. Rep. 6:420; JAMESON Synops. Pl. Aequat. 2:197.

Ecuador: Quito, at Mount Loja, JAMESON; HARTWEG 795; Colombia: Without locality, MORITZ 478; St. Martha (1844) PURDIE (in herb. Stockholm).

27. B. DECORA Drake in Morot, Jour. de Bot. 3:71. 1889.

Ecuador: Chonta-Cruz, POORTMANN 116: Colombia: In the province of Rio Hacha, LINDEN 1618.

CORYMBOSAE

28. **B. congesta,** sp. n., Frutex: rami cinerei, raro pilosi, ramulis hispidis canis, dense foliosis: folia conferta, coriacea, rigida, valde revoluta, margine serrato-ciliata, utrinque hispida, setis longis basi tuberculatis vestita, lanceolata, 5 mm. lata, 15 mm. longa, basi rotundata, apice acuminata, acuta, nervo medio supra impresso (subtus prominulo, setoso) avenia, breviter petiolata, petiolis hispidis: racemi subcorymbosi densi, multiflori, pedunculis pedicellisque ferrugineo-hirtis: pedunculi breves, pilosi, crassi, pedicellis breves, 5–8 mm. longis, calyce paulo longioribus: bracteae binae ad pedicelli basin dispositae, lineares, pilosae: calyx campanulatus petalis quintuplo brevior, 7-lobatus, pubescens, lobis ovatis, obtusis, fere usque ad basin liberis, biseriatis, 5 mm. longis, 3 mm. latis: flores magni, petalis 7 oblongis, obtusis, 2.5 cm. longis, 5–7 mm. latis, apice pubescentibus: stamina 14 basi dilatata et pilosa, petalis subaequilonga: Stylus exsertus crassus, stigmate magno capitato: ovarium septisulcatum.

Venezuela: Without precise locality, FUNCK and SCHLIM. Allied to *B. myrtifolia,* but differs in its obtuse calyx lobes, stout and short pedicels and small bracts.

29. **B. lehmanniana,** sp. n.—Fruticosa: rami cinereo-pilosi, ramulis ferrugineo-tomentosis, dense foliosis: folia conferta, coriacea, lanceolata 1.5–2 cm. longa, utrinque attenuata, petiolata, margine revoluta, supra lucida et cinereo- et ferrugineo-hispida, subtus dense ferrugineo-tomentosa, petiolis hispidis: racemi brevissimi, subcorymbosi, densi, pedunculis pedicellisque ferrugineo-tomentosis, pedicellis crassis circa 1–1.2 cm. longis, bracteis forma foliis valde

similibus: calyx campanulatus, amplus, 7-lobatus, 6 mm. longus, pubescens, lobis angustis, acutis, quam petalis 8-plo brevioribus, biseriatis: petala 7 oblonga, obovata, obtusa, apice (vel juvenilia omnino) pubescentia, 0.8–0.9 cm. lata, 3.5–4 cm. longa: stamina 14 basi dilatata pilosa, petalis vix longiora: stylus crassus, longe exsertus; stigmate 7-partito magno.

Colombia vel Ecuador, loco non indicato, LEHMANN 4962.

A very distinct species, perhaps nearer to *B. cinnamomea* than to any other; from this uncertain species it differs in the form of inflorescence and in its much larger flowers.

30. **B. grisea,** sp. n.—Frutex: rami ramulique griseo-tomentosi: folia approximata coriacea, rigida, elliptica, basi rotundata in petiolum vix attenuata, apice obtusiuscula, semper brevissime et obtuse mucronata, 20 mm. longa et 12 mm. lata, supra lucida, hispida vel glabriuscula, subtus glauca, dense albofulvoque pubescentia, margine leviter revoluta et integerrima: racemi terminales, simplices, subcorymbosi, laxi, parviflori, pedicellis crassis adpresse griseo- vel ferrugineo-tomentosis, 1.5 cm. longis; bracteis foliiformibus pedicelli $\frac{3}{4}$ aequalibus: calyx campanulatus amplus, 7-lobatus, lobis latis, ovatis, obtusis, pilosis, omnino liberis, 6 mm. longis et 4 mm. latis, quam petalis 5-plo brevioribus: petala 7 oblonga, obovata, apice obtusa et pubescentia, 2.5 cm. longa, 8 mm. lata: stamina 14 basi dilatata pilosa: stylus crassus, exsertus, stigmate magno.

Colombia (New Granada): Without precise locality, FUNCK and SCHLIM 14751. A very distinct species, unlike any other.

31. B. CAXAMARCENSIS H.B.K. Nova Gen. **3**:230; DC. Prodr. **6**:731.

Peru: In the Andes of Caxamarca, HUMBOLDT.

32. B. MYRTIFOLIA Hérincq in Rev. Hortic. **4**:182. 1857.

Colombia (New Granada): Province of Bogota, LINDEN 773; KARSTEN.

33. B. COARCTATA H.B. Pl. Aequin. **2**:125; H.B.K. Nova Gen. Am. **3**:228; DC. Prodr. **7**:731; Wedd. Chloris And. **2**:183. 1857; Walpers Ann. **2**:1123; Paxt. et Lindl., Flower Gard. **1**:83; VAN HOUTTE, Fl. des Serres **4**:3286; non *B. coarctata.* Hook. Bot. Mag. t. 4433; *Acunna lanceolata* Cav. ex DC. Prodr. **7**:731.

Peru: Paramo de Janaguanga, near the town Caxamarca; Colombia: Pasto, at the Borboncillo, February, 1881, LEHMANN 564; without precise locality, FUNCK and SCHLIM 1600.

34. B. PHILLYRIAEFOLIA Benth. Pl. Hartweg. 225; Walpers Repert. 6:420; Wedd. Chloris And. 2:182. 1857.

Colombia: Province of Popayan, HARTWEG 1231; Cauca, 1700 m. alt., Aug. 16, 1881, LEHMANN 823.

35. **B. popayana**, sp. n.—Frutex, ramis ramulisque tomentulosis: folia conferta, coriacea, rigida, oblongo-elliptica, obtusiuscula vel acuta, apice breviter calloso-mucronata, distincte petiolata, 3–3.5 cm. longa, venis distinctis perspicuis, nervo medio supra sulcato et villoso, subtus prominulo et parce tomentoso: inflorescentiae racemus subcorymbosus, solitarius, apice ramulorum dispositus, brevis, parviflorus, floribus magnis 5–8: pedunculus subnullus pedicellique ferrugineo-tomentosi, pedicelli parvi 8–10 mm. longi, bracteis linearibus, 3–5 mm. longis, ferrugineis: calyx campanulatus, amplus, 7-lobatus, tomentosus vel subglaber, lobis late ovatis, obtusis, margine ciliatis: petala 7 omnino pubescentia, 4 cm. longa, circa 1 cm. lata, oblonga, apice rotundata: stamina 14 libera, basi dilatata pilosa, petala $\frac{1}{4}$ excedentes: stylus longissime exserta, stigmate magno, 7-partito.

Colombia: Popayan, KARSTEN.

Allied to *B. phillyriaefolia*, from which it differs in the pubescence of the petals, in dimension of the flowers, and in the very short peduncle.

36. **B. corymbosa**, sp. n.—Frutex, ramis ramulisque tomentulosis: Folia coriacea, rigida, oblonga, apice obtusiuscula, brevissime callosa, distincte petiolata, 3 cm. longa, 1–1.5 cm. lata, glabra, subtus glauca, supra lucida, venis distinctis, perspicuis, nervo medio supra sulcato et villoso, subtus prominulo et parce tomentoso. Inflorescentiae corymbosae corymbus solitarius, apice ramulorum dispositus, brevis, parviflorus, floribus magnis: pedunculus brevis pedicellique ferrugineo-tomentosi, pedicelli 1–1.5 cm. longi; bracteis lanceolatis foliiformibus pedicello aequantibus: calyx campanulatus, amplus, 7-lobatus, breviter ferrugineo-pilosus, lobis late, ovatis, apice attenuatis, margine ciliatis: petala 7 glabra, margine ciliata, 2 cm. longa, 0.7 cm. lata, oblonga, apice rotundata: stamina 14 libera, basi dilatata pilosa, petala $\frac{1}{4}$ excedentes: stylus exsertus, stigmate magno 7-partito.

Colombia: Pasto, Venta Menes, KARSTEN.

Allied to *B. popayana*, from which it differs as to its glabrous petals and in the dimension of its bracts, which are equal to the pedicels.

IMPERFECTLY KNOWN SPECIES

37. B. CINNAMOMEA Lindl. in Garden. Chron. 1848.—We have no specimen of this species in our herbarium, and we know it only by the short description given in Flow. Gard. 1:86.[4] It seems to be near to *B. lehmanniana*, which differs by its large flowers and corymbose inflorescence.

38. B. SCHOMBURGKIANA Klotsch in Schomb. Reisen in British Guiana 3:1088; BROWN in Trans. Linn. Soc. 6:10. In both works only the name is mentioned.

Guiana, Humiruda, and southern declivity of Mount Roraima 6000 ft., R. SCHOMBURGK.

39. B. TRICOLOR Linden ex Hérincq, Rev. Hortic. 4:185.—This is the diagnosis given by HÉRINCQ: "The plant has the branches ferrugineous and the leaves blazing. The flowers are very pretty, white and pink with yellow spots at the base of the petals." It is too short to permit of definite conclusions as to the precise status of *B. tricolor* in the system of Bejarias.

DOUBTFUL SPECIES

40. B. FLORIDANA Gdgr. Sertum plantarum novarum in Bull. Soc. Bot. France 65:56. 1918.—The description given by GANDOGER is too brief and appears to be only a comparison with *B. racemosa:* "a *B. racemosa* recidit ramis novellis non hispidis, foliis oblongis majoribus, pedunculus viscosis bracteis multo brevioribus fructuque magis depresso. Folia coriacea, glauca inte[illegible]rrima." The author states it to be more frequent than *B. racemosa*. It is possible that this species is only a variation of *B. racemosa*, but we feel certain that in many respects it differs decidedly from *B. racemosa*.

41. B. PARVIFOLIA Rusby, Bull. N.Y. Bot. Gard. 8:110. 1912.—We cannot detect the difference between this species and *B. glauca* H. et B. We have not seen the specimen collected by WILLIAMS, but the description is quite identical with the one by HUMBOLDT.

JARDIN BOTANIQUE PRINCIPAL
LENINGRAD, U.S.S.R.

[4] "Branches downy and hispid; leaves slightly downy above covered beneath with thick ferruginous wool. Flowers in a close terminal panicle, with very woolly and hispid stalks, and calyces. Its flowers are smaller than in *B. aestuans*, and are arranged in a close panicle."

ANATOMY OF LYCOPODIUM SPORELING

EARLE AUGUSTUS SPESSARD

(WITH PLATES IX, X, AND NINE FIGURES)

Material

The material of *Lycopodium lucidulum* Michx., on which the following account is based, was found in the vicinity of Marquette, Michigan in 1918. Several hundred sporelings of this species, ranging in length from 1 mm. to 4 cm., comprise the collection. So far as can be determined, these sporelings were not more than two years old. This series appears to be complete enough to show all the stages of growth between the embryo and the typical adult colony, but such is not the case. It is not difficult to find young colonies of *L. lucidulum* with the individual plants no longer than the sporelings mentioned, but close examination shows that these plants are derived from the well known vegetative gemmae shed in great numbers by many adult plants. One gemmaling may give rise to an entire colony of adults, through branching and a subsequent fragmentation of the stoloniferous stem at its base. In view of this fact, the series of sporelings found seems complete enough to establish a connection between sporeling and adult, but since this connection was not made, an explanation must be attempted.

The most obvious explanation for the discrepancy would be that the later stages were merely overlooked, and this would be entirely justifiable were there no other facts to be considered. Briefly, then, a number of observations will be mentioned. First, the shape and color of the adult plants and gemmalings are the same. The sporeling is lighter in color, and the diameter of the stem tapers from the apex downward to the foot and roots. The sporeling, even at its greatest length, is a much more delicate plant than the gemmaling, which is stockily built. Second, the sporelings grow in drier ground than do either the gemmalings or the adults, and they die in great numbers because there is not enough moisture. The gemmalings almost invariably die also when they germinate in the drier places where

sporelings are found. On the other hand, the gemmalings thrive in the moister ground, where the sporelings find it difficult if not impossible to mature.

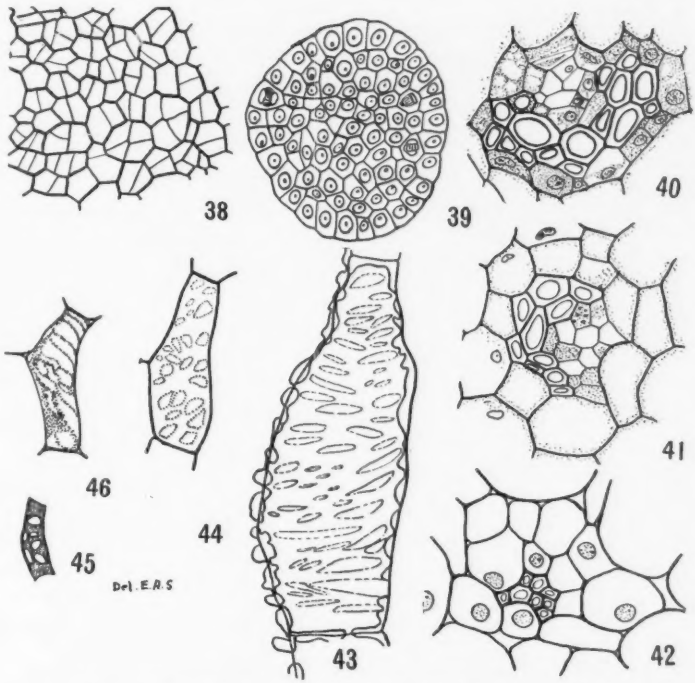
These observations force the conclusion that *L. lucidulum* is almost if not quite ecologically incapable of using the sexual process for survival. Physiologically the plant is entirely efficient sexually; but the products of the process, the sporelings, die because they cannot survive the environment. The adult colonies of *L. lucidulum* are rarely if ever the result of sexual reproduction. In the experience of the writer the transition from sporeling to adult has never occurred. In the following description of the anatomy of the sporeling of this species of *Lycopodium*, it will be clear to those acquainted with the stele of the adult plant that there are many points of difference. The writer is now investigating the anatomy of the gemmalings in the hope that some of the discrepancies may be accounted for.

Stele

The apical meristem extends downward in the stem to a distance of about 70 μ. It is composed of an actively dividing epidermis and an inner fundamental tissue. The whole may be further divided into an apical group extending down to the 15 μ level, and a subapical group extending downward to the 70 μ level. In the apical group (fig. 38) the cells divide in three planes in both the epidermal and fundamental regions. In the subapical group (fig. 39) the divisions are in three planes in the epidermis, but largely in two planes in the fundamental region. There is dermatogen, but no plerome-periblem group. Histologically the stele arises as a direct modification of the cells of the fundamental region. The cortex is derived from the same tissue simply through not becoming differentiated. In none of the sporelings was the writer able to demonstrate an endodermis, although a very definite demarcation exists between cortex and stele. At a level of about 80 μ the entire fundamental region, with the exception of a few cells at the periphery, stains as a desmogen strand. The cortex of the stem lower down appears to have been derived largely from the dermatogen and less from the fundamental region.

The adult stele consists of pericycle, xylem, phloem, and pith. The cells of the pericycle are elongated and contain protoplasm.

The left hand cell with nucleus in fig. 25 is from the pericycle of a stem. The end walls of cells lying within the pericycle usually are



FIGS. 38–46.—Fig. 38, section of stem 15 μ from tip; fig. 39, section of same stem as in fig. 38, 70 μ from tip; fig. 40, section of same stem just above primary root and foot; fig. 41, section of root of same plant just below foot; fig. 42, section of leaf; fig. 43, foot cell of sporeling; fig. 44, prothallial cell from conducting region and near foot; fig. 45, portion of phloem cell in sporeling stele near foot; fig. 46, young xylem cell; figs. 38, 39, ×350; figs. 40–46, ×775.

diagonal, while those of the pericycle usually are not. Figs. 28 and 30 show the extent of the pericycle. In the former the xylem abuts on the cortex in some places. The pericycle cannot be considered as a definite sheath inclosing the balance of the stele.

The major portion of the stele is occupied by xylem. Figs. 1–24 show this element in heavy black, with the limits of the stele proper

indicated by a broken line. The extent of the xylem is shown for the stem in figs. 25, 27, and 28; for the root in figs. 31–33; for the leaf in fig. 42.

The preparations from which figs. 28, 30, and 32 were taken to illustrate phloem are so unsatisfactory that this element of the stele must be left for further investigation. That these thin-walled cells are phloem I am certain, but the details of their structure are doubtful. The phloem groups lie on radii and on a circumference different from those on which the protoxylem strands arise. In *L. lucidulum* phloem is not only less extensive than in higher plants, but its differentiation seems to be delayed.

The word pith has been used here for want of a better term. A glance at figs. 26 and 28 shows a group of large elongated cells within the stele, which were derived from the fundamental region of the subapical group of cells, and which have not differentiated into any stelar element to which they can be referred. If this plant could have been examined after it had grown several more years, perhaps we should find these cells differentiated into xylem or phloem. The cells are stelar in origin, are to be considered as stelar elements, and in view of what will be said about them in the discussion at the end of this paper, will be called pith.

Leaf and stem

TURNER has shown for the adult of *Lycopodium*, and STOVER for grasses, that the leaf strand is first differentiated in the leaf itself, and later makes connection with the stem group. My preparations confirm this in the juvenile stages of *L. lucidulum*. While the phyllotaxy of this species is not constant, there exists a very definite relationship between the leaf trace and the locus of metaxylic differentiation. This interesting feature will be presented in a separate paper.

The protoxylem of the stem is laid down on four, five, or six radii, as shown in fig. 28. The metaxylem develops centripetally, and in a very regular sequence of units related to the leaf traces. The mass of metaxylem appears to be very irregular, as shown in figs. 1–24. This irregularity is due to the presence of adventitious roots.

Primary root

The stele of this organ is essentially like that of the stem, except that there is not the disturbance due to leaf and adventitious root formation. Fig. 24, from the primary root of an old sporeling, may be compared with fig. 32 from the middle stem region of a young sporeling. The metaxylem of the two strands arises by a process of differentiation between two protoxylem strands. Why the root xylem should appear similar to the stem xylem in form is difficult to explain. The stem metaxylem is laid down in definite relation to the leaf traces, but the same pattern results in the primary root, where there are no leaves.

Adventitious roots

These roots are very remarkable. They were called internal roots by STRASBURGER, and were studied by Miss STOKEY in *L. pithyoides*. A complete bibliography of the work done previously will be found in her paper. While not as abundant as in *L. pithyoides*, they are plentiful enough to give the primary root of *L. lucidulum* only temporary significance. They arise sometimes within a millimeter of the stem tip, absorb the cortex of the stem, and push their way down through it to within a millimeter of the primary root and the foot of the sporeling. There they emerge and pass into the soil. An adult plant and a large sporeling have masses of these roots at the base. If, every time a new adventitious root appeared, we were to amputate all of the plant but it and the region above it, we should see a plant not unlike the very young sporeling with a primary root. The whole process simulates a condition which looks like a perpetual recapitulation of the early sporeling stage.

The adventitious root begins as a proliferation of pericycle cells. A cap is produced normally. When about half a millimeter long the stele is clearly differentiable. The subsequent xylem of this new root finally connects with the neighboring edges of two xylem crescents in the stem (fig. 14), or, more frequently, with the ends of a single crescent (fig. 35). The stem xylem does not contribute to the xylem of the root. It is very easy to fancy that we observe the stem xylem bending downward and outward to enter the root, but close

examination shows that between the mature stem and root xylem there lies an immature group of cells in the process of being transformed into xylem. Figs. 1–22 show the origins of five adventitious roots in a typical sporeling. The crescents of xylem in the stem are constantly being shifted about. If the stem xylem were removed bodily, it would show a very ragged appearance. In any given vertical line there are many gaps in the xylem, places where the fundamental stelar tissue has not formed xylem. These are not leaf gaps, which are definite in their positions; they are places where no differentiation into specialized xylem has occurred.

Leaf, stem, and root develop their xylem *in loco*, and later connect. The sequence of events is the same in each case. From an acropetal meristem there is developed a primary stele, which, in the case of the stem, occupies nearly the entire diameter. From this as a beginning, the types of stele which may develop are either a radial, a collateral, or a concentric.

Conducting parenchyma

The cortical cells of the root and stem have thick walls with pits. In some cells whose walls stain deeply with anilin blue, smaller white slits appear under a magnification of about 1500 diameters. It is doubtful whether these are perforations entirely through the wall, although the technique used has made it appear so. The inner cells of the foot (fig. 43), the epidermal cells, and even the cells of the prothallium into which the foot projects, all have pitted walls. The epidermal cells of the foot are also glandular and contain starch.

From the stele of the stem at the foot region, through the foot itself, thence into and through the central region of the prothallium, there extends a system of conducting cells provided with pits. Below this lies the fungus region. This relationship is not without significance. From soil to sporeling there is a direct line of communication in the form of a conducting mechanism adequate for the translocation of food.

Several things are known regarding the situation: (1) The prothallium seems to require the fungus, for it will not grow without it in the cases examined. (2) Carbohydrate is stored in prothallia entirely devoid of chlorophyll. Whether this carbohydrate comes from

the soil as such, or is synthesized from materials brought into the prothallium by the fungus, is not known; that the source is in this direction is hardly doubtful. It is important to mention that in epiphytic and surface forms that possess some chlorophyll in the prothallia, there is a less extensive invasion of the fungus. (3) The sporeling uses this supply of food, together with the entire protein content of the prothallium, absorption taking place through the foot. This absorption is so complete that prothallia are often found consisting only of the epidermal hull, the fungus lining it, and the sporeling foot still adhering to the inner portion of the withered mass. An excellent confirmation of this was found in the sporeling shown in fig. 37. This sporeling possessed no primary root whatsoever, and therefore had to reach its state of maturity entirely at the expense of the prothallium. Adventitious roots had developed within the cortex, but none had broken through it to reach the soil.

Here, then, is a definite symbiotic requirement with a definite anatomical mechanism to meet it: the fungus supplies the prothallium, and the prothallium supplies the sporeling with food. Until the chemical changes between the three organisms are determined, it cannot be stated whether this is a case of parasitism or of symbiosis; I have merely attempted to show that there is a mechanism present for the transport of materials from soil to sporeling.

Discussion

The writer has purposely avoided speaking literally of the "fusion" and the "splitting" of xylem, since it is doubtful whether these terms can be used with any degree of accuracy here. When xylem develops at one place and fails to develop at another, as shown in figs. 6 and 7, a condition is presented which makes it appear that splitting has occurred; or, as in figs. 8 and 9, that fusion has taken place. If a clay model were made of the stele of *L. lucidulum*, with xylem shown in red, and the fundamental stelar tissue shown in blue as a background, many blue patches would appear where the xylem failed to appear. These patches are areas of arrestation. Xylem cells do not shift about; they are differentiated at the spots where the cells from which they are transformed were laid down. In places where these cells are not transformed we have

merely to do with an omission, and not with a splitting. This is a polyxylic phenomenon, and might conceivably have some bearing on the matter of polystely, but it is not a phenomenon brought about by the breaking up of an antecedent stele; it is due to the omission of xylem activation, whatever may be the cause of that.

The history of vascular ontogeny may be interpreted from both ends of a plant at the same time. Undifferentiated meristem changes into elongated parenchyma, and this into prosenchyma. This is a longitudinal differentiation. Beyond this point differentiation is strictly lateral, except where longitudinal differentiation is renewed in the formation of adventitious roots or of lateral buds. Lateral differentiation takes place on definite circumferences and on certain radii. Definite regions of the pre-stele are to become xylem, phloem, pericycle, or none of these. I wish to make it clear that xylem, for instance, is not to be interpreted as an errant invader capable of splitting and of growing in several directions; it is a fixed stage in ontogeny. The early protoxylem becomes a significant point of reference, not merely to the anatomist but to anatomy, for the loci of the early elements must be radial, and may be near or away from the center of the stele, furnishing the starting points for exarch, mesarch, or endarch structures. This variation in the radial location of protoxylem is the critical phase in stelar ontogeny. After it is established, it is a matter of indifference as to the type of stele capable of being developed from it. In the sporeling of *L. lucidulum* several phases are encountered. A radial protostele passes into a collateral protostele; this in turn may become a concentric protostele with internal phloem, an amphivasal protostele. Again, it may pass into a monocollateral or a bicollateral protostele. Here is a vascular "No man's land." This is precisely what we should expect in *Lycopodium*, since the genus is an ancient one. It stands at the cross roads of stelar development, unable to advance.

The sporeling of *L. lucidulum* offers some evidence concerning the origin of pith. JEFFREY claims that this tissue is cortical in origin; VAN TIEGHEM, BOWER, and others claim that it is stelar; this investigation confirms the latter view.

It was mentioned in a previous paragraph that where xylem does not differentiate in the stelar tissue there remains a gap. The xylem shifts with regard to our view of it, but it neither moves its position

nor splits. These gaps are present before and after the appearance of adventitious roots. The cells in these gaps are prosenchymatous, that is, stelar in nature. The gaps are not holes left by a moving xylem to be filled in by an accommodating cortex.

So long as a cell has not lost its plasticity, we may expect to observe it returning to the functional behavior of its meristem forbear. There comes a time in the process of differentiation, however, when it is impossible for the cell to turn back; it is fixed as it were. The cell may be stopped in its development, and thus fail to complete a destiny; it may turn at some stage from one function to another, but the new function must lie within the limits of the plasticity of the protoplasm of the cell at that moment. Herein lies the difficulty in attempting to interpret the pith as cortical in origin. Cells from the outer circumferences of the cortex and of the stele do become meristematic to the degree of producing new stems, leaves, and roots. In all cases, however, these cells are not extremely removed from meristem of some nature lineally. At the younger levels, where such a phenomenon as a cortical invasion would have to take place, the stelar cells are as plastic as the cortical. At the lower levels, where the xylem has differentiated to leave the gaps, the cortex cells have thick cell walls, and have less protoplasm than is seen in meristematic tissue. It is doubtful whether we can point to definite cells of the subapical region in *L. lucidulum* and assign to them a certain destiny. It may be true that physiologically it is a matter of indifference to the cells, but as differentiation proceeds, this indifference decreases or becomes less pronounced. The ontogenetically older cells are less plastic; those in the cortex are cortex and those in the stele are stele. The ability to return to the meristem condition has disappeared. If we were to imagine that pith is derived from cortex, we are faced with the phenomenon of a fully differentiated structure invading another fully differentiated one, and becoming an integral part of that structure without creating the least physical disturbance. Roots have been seen to invade cortex, however, and this invasion is announced by a great display of cortical disintegration. There is no doubt to the observer that an invasion is taking place, but when we try to imagine a cortex invading a gap left in the stele, we find it too orderly to evade suspicion.

The word gap is a good one, implying a place where something

has been left out, while a hole implies that something has been taken out. Cortex was never left out or taken out of a stelar gap, for cortex was never there. Undifferentiated stelar elements were there from rather early ontogeny. It is more sensible to interpret the gap as a spot of potential xylem, which, not yet past its period of plasticity, was called from one function to another. It follows naturally that if the gaps are stelar in origin, the pith cannot be cortical in origin. As potential stele, the pith is that portion in the stelar region which is plastically indifferent as to its future. At some place in ontogeny, physiological requirement demands that it be not vascular at all. It does not cease to be conductive, it never reaches that state. This interpretation does away with the mechanical difficulties involved when we try to imagine one tissue invading another. Furthermore, if pith is not potential stele, we are presented with an anatomical paradox in the isolated conductive strands sometimes found in pith.

The writer wishes to express his thanks to Professor W. J. G. LAND of the University of Chicago for his criticisms in the preparation of this paper.

Summary

1. The stele of the sporeling of *Lycopodium lucidulum* is a protostele which is never solid, but may have the elements arranged concentrically or collaterally.

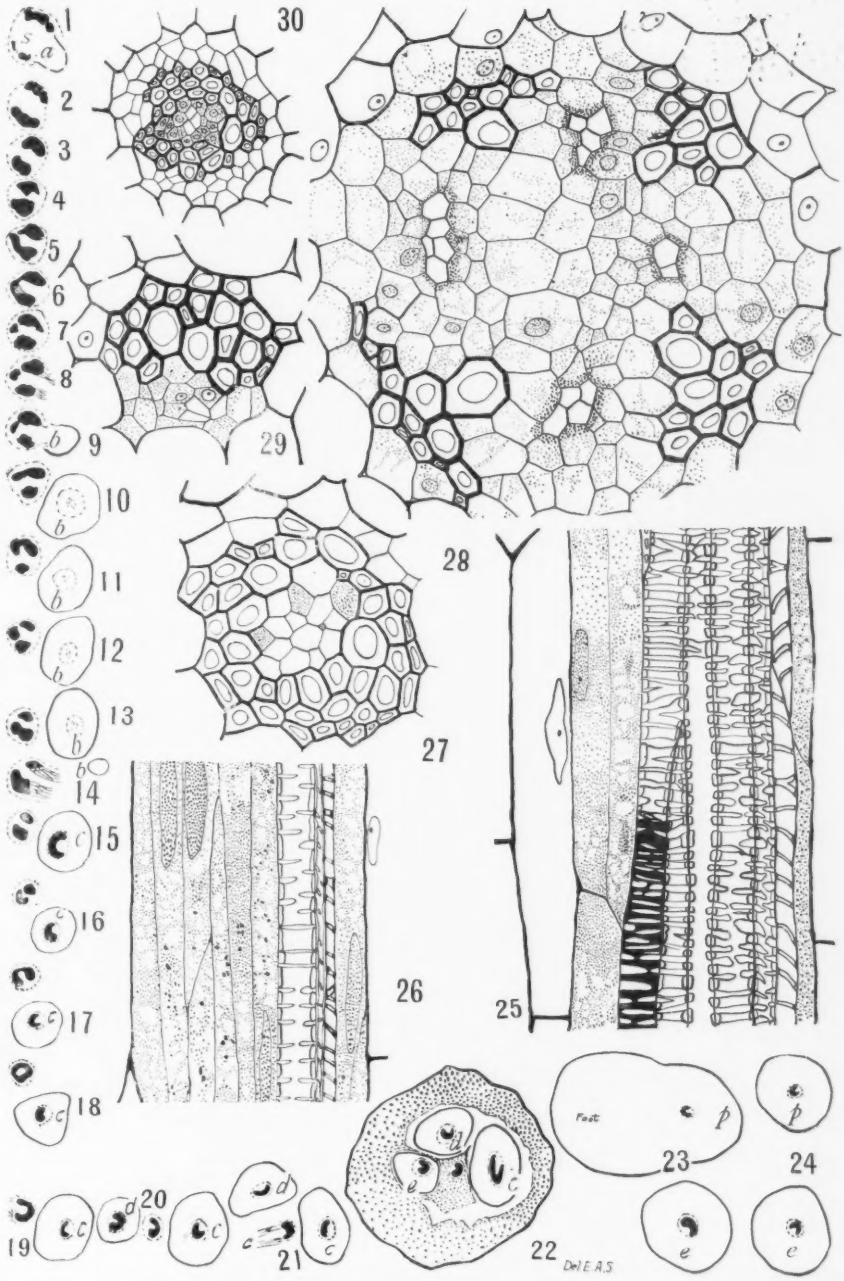
2. There is no well defined endodermis. The phloem is not very far advanced, has not been worked out carefully, but appears to be at first radial and later less definite.

3. The xylem is radially arranged at first, and later forms crescent-shaped slabs or a complete ring.

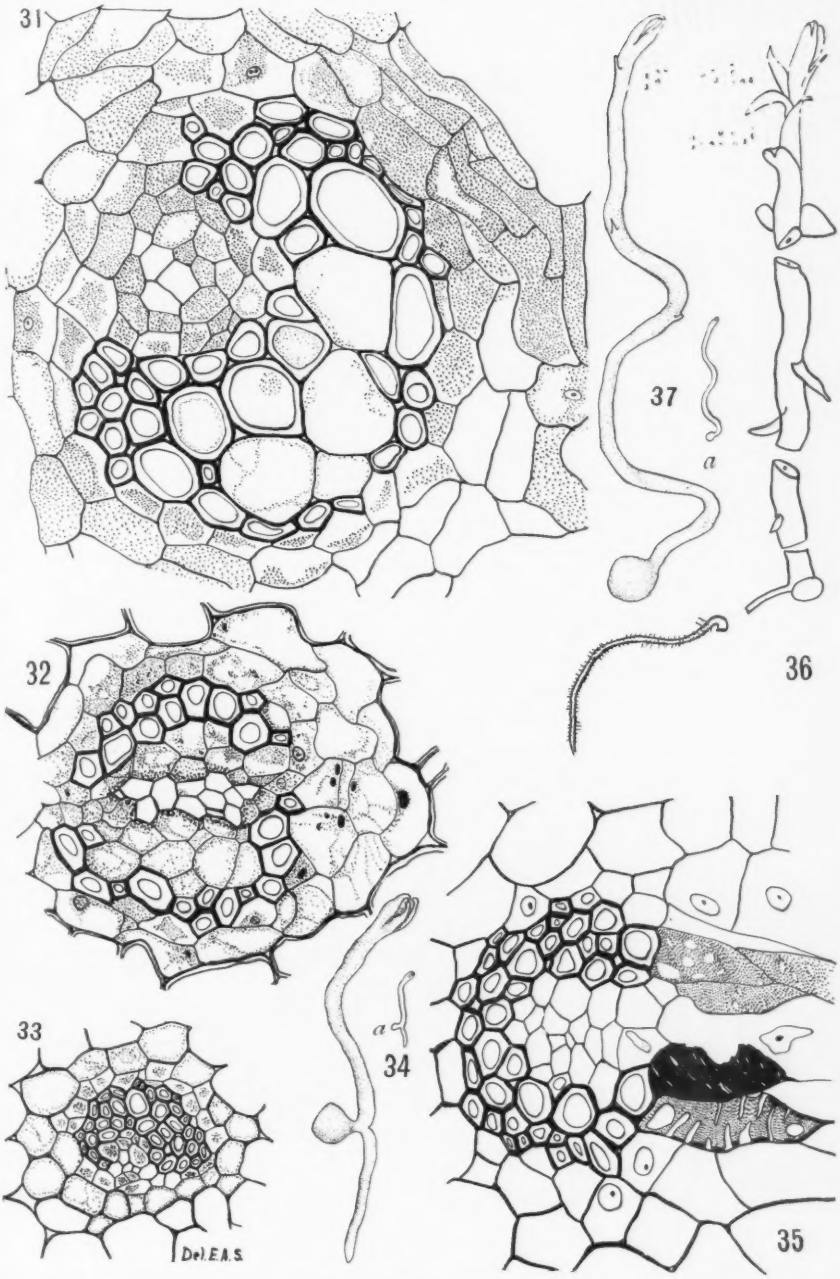
4. The xylem is developed independently in root, leaf, and stem; these are later joined.

5. There is no splitting or fusion of xylem in a literal sense.

6. Gaps in the xylem are interpreted as not due to an invasion of cortex, but as an arrestation in early ontogeny, causing the cells of the stele to be diverted from one function to another. Pith is put in the same category.



SPESSARD on LYCOPODIUM



SPESSARD on LYCOPODIUM

7. Cortex and stele are differentiated almost if not quite as far back as the initials.

8. The phyllotaxy varies with individuals, and has an apparent determinative influence on the form of the stem xylem.

9. The adventitious roots appear acropetally, and pass down through the cortex, emerging near the foot.

10. There is an adequate conducting apparatus from the stele of the sporeling to the fungus region of the prothallium. The sporeling may derive some of its food through the endophytic fungus by way of the prothallium.

OUACHITA COLLEGE
ARKADELPHIA, ARK.

[*Accepted for publication September 21, 1927*]

DESCRIPTION OF PLATES IX, X

PLATE IX

FIGS. 1–24.—Sections of stele of stem and adventitious roots, from point a few millimeters below stem tip down to about middle of primary root: *s*, stele of stem with xylem in heavy black and limits of stele indicated by broken line; roots (labeled *a*, *b*, *c*, *d*, *e*) surrounded by continuous line; each figure shows stem stele, and most of them one or more roots, which lie within cortex of stem; cortex not shown except in fig. 22, after which roots have passed out to enter soil; *p*, primary root; *a*, youngest adventitious root; *e*, oldest root; ×150.

FIG. 25.—Longitudinal section of stem; ×775.

FIG. 26.—Longitudinal section of root; ×775.

FIGS. 27–30.—Cross-sections of stems: condition in fig. 28 is generally found near apex, but this section was taken just above primary root, phloem (unshaded cells) is on radii alternating with xylem radii, and on a different circumference (this is not always true); fig. 29 shows section from same region in another plant; figs. 27–30, ×775; fig. 30, ×375.

PLATE X

FIGS. 31–37.—Figs. 31–33, cross-sections of roots; fig. 31, adult adventitious root from mature plant; ×775; fig. 33, adventitious root of sporeling after emerging from cortex; ×375; fig. 32, middle of primary root of sporeling; ×775; fig. 35, xylem connection at junction of adventitious root and stem xylem; ×775; figs. 34, 36, 37, three sporelings, one without primary root, a rare condition; fig. 36 shows method of cutting long and crooked specimens for sectioning; ×5, with duplicates to right natural size.

WATER-SOLUBILITY OF DRY MATTER IN RELATION TO CALCIUM NUTRITION OF NORMAL ORANGE AND LEMON LEAVES[1]

A. R. C. HAAS

Introduction

It has been shown by KELLEY and CUMMINS (**2**), and later repeatedly confirmed by the writer, that normal mature leaves of trees of lemon and Washington Navel and Valencia orange differ very little in percentage of ash, and that this ash contains approximately 30–35 per cent of calcium. A study, therefore, of the narrow range of the sodium, potassium, calcium, and magnesium percentages in the ash of normal mature citrus leaves gives us very little opportunity to gain an understanding of differences in the behavior of the trees when subjected to the same external conditions. Numerous ash analyses of normal mature leaves of lemon and Navel and Valencia orange trees have failed to show any fundamental differences in the nutrition of these leaves.

Water-solubility studies conducted by REED and HAAS (**3**), upon the dry matter of normal Valencia orange trees grown in soil, have shown that approximately one-half of the calcium present is water-soluble, the ash of the water-soluble fraction being approximately 57 per cent. The water-solubility studies were restricted to Valencia orange trees, because it was believed that the analyses would show no important changes if they were also conducted upon any of the other varieties of citrus. After several years of soil, sand, and water-culture studies, made chiefly upon Valencia orange trees, the writer became concerned regarding the uniformity of the ash analyses of the various citrus varieties in relation to the diversity of the behavior of the trees. Had the ash analyses of the citrus varieties been somewhat different from one another, the present study would have suggested itself much earlier.

In this investigation it has been found that the ash of the water-

[1] Paper no. 175, University of California, Graduate School of Tropical Agriculture and Citrus Experiment Station, Riverside, California.

insoluble fraction of the dry matter and the water-solubility of the calcium of normal mature lemon leaves are decidedly different from those of Navel and Valencia orange leaves, and that the age of the leaf determines in a large measure the water-solubility in a given variety.

Investigation

The samples of leaves were collected from the trees in the experimental plots at the Rubidoux tract of the Citrus Experiment Station. The leaves were dried at 70–80° C. and finely ground. Samples of 10 gm. each were weighed into 150 cc. pyrex beakers, and the beakers then filled with distilled water and left to stand over night. The following morning the solutions were filtered and the leaf material transferred to the filter papers, where they were leached with successive small amounts of distilled water until a volume of about 500 cc. of filtrate was obtained. The filter paper and its contents were dried and ashed by igniting in a weighed dish at low heat, leaching out the soluble salts, drying, and reigniting the filter paper until free from carbon. The added soluble-salt solution was then evaporated and gently ignited to constant weight. The filtrate was evaporated nearly to dryness, transferred to a weighed dish on a hot plate, and when near dryness was placed in an electric oven at 100° C. to complete the drying process. The dried mass was then ignited at low heat, the soluble salts leached out and reignited, and treated as previously described. A point of interest in this connection was the fact that the dried water-soluble fraction of immature lemon leaves puffed up enormously on being ignited.

The ash of the water-soluble and that of the water-insoluble fractions were dissolved in dilute nitric acid, and after being filtered the solutions were made up to a volume of 500 cc. Calcium and magnesium were determined in each case, and in some cases sodium and potassium were also determined. The total phosphorus extractable with distilled water from the dry matter was determined by means of oxidizing the organic matter with magnesium nitrate.

Table I gives data in regard to the ash of the water-soluble and water-insoluble fractions of the dry matter of lemon leaves of different ages, and the water-solubility of the bases. The ash of the water-soluble fraction varies within a narrow range, lying between 3.5 and

TABLE I

WATER-SOLUBILITY OF DRY MATTER OF NORMAL LEMON LEAVES OF DIFFERENT AGES, EXPRESSED AS PERCENTAGE DRY MATTER

Locality (Rubidoux tract)	Age	No. of leaves	Weight		H_2O content as percentage fresh weight	Ash of		Calcium		Soluble as percentage of total	Magnesium		Soluble as percentage of total	Soluble as percentage of total sodium	Soluble as percentage of total potassium	Phosphorus	
			Fresh gm.	Dry gm.		Soluble fraction	Insoluble fraction	Soluble	Insoluble		Soluble	Insoluble				Soluble	Insoluble
	Collected June 22, 1927																
Plot B, Eureka on sweet orange stock	Young	268	76	19	75.00	4.91	2.32	0.463	0.788	37.01	0.219	0.058	79.06	84.09	98.14	.....	.....
	Full sized, thin	160	134	34	74.62	4.09	4.31	0.379	1.501	21.06	0.164	0.120	57.75	76.93	90.87	.....	.....
	Nearly mature	100	120	48	60.00	4.71	11.36	0.813	3.939	17.11	0.151	0.061	71.22	75.84	96.23	.....	.....
Plot U, Eureka on grapefruit stock	Young	575	58	16	72.41	5.15	1.45	0.470	0.424	52.57	0.263	0.063	80.68	.....	.....	.....	.....
	Full sized, thin	141	107	30	71.96	3.53	3.63	0.271	1.238	17.95	0.176	0.123	58.86	.....	.....	.....	.....
	Mature	74	98	44	55.10	4.55	11.47	0.935	4.307	17.84	0.264	0.073	78.34	.....	.....	.....	.....
	Collected April 25, 1927																
Variety Block, Belair lemon on sour orange stock	Young	350	65	17	73.85	5.37	2.22	0.273	0.725	27.35	0.202	0.088	70.00	.....	.....	0.425	0.045
	Full sized, thin	200	145	33	77.24	4.72	3.43	0.222	1.089	16.93	0.139	0.142	49.46	.....	.....	0.383	0.045
	Mature	100	140	59	57.86	4.36	11.22	0.903	4.266	17.47	0.216	0.107	66.87	.....	.....	0.175	0.044

5.4 per cent of the dry matter, and appears to be slightly lower in mature than in very young leaves. The ash of the water-insoluble fraction increases with the age of the leaves. When the leaves are full sized but thin, the two fractions are more nearly equal in ash content than at any other time in the development of the leaves. As the leaves become mature, the ash of the water-insoluble fraction increases rapidly, while that of the water-soluble fraction remains practically unchanged. Table I shows that the very young leaves contain approximately the same percentage of water as do those that are full sized but thin, while there is a decrease as maturity is approached.

The water-insoluble calcium of the dry matter increases gradually at first and most rapidly as maturity is approached, but changes very little after maturity is reached. There is some reason to expect that a curve showing the water-insoluble calcium, plotted against the age of the leaves, would follow the usual course of growth curves, although this has not been carried out as yet on citrus. The water-soluble calcium of the dry matter decreases slightly as the leaves become full sized but thin, and then increases toward maturity of the leaves. Calculations from the data have shown the usual increase in percentage of total calcium in the total ash with increasing age of the leaves. In table I, however, the insoluble calcium increases at a more rapid rate than the soluble calcium, with the result that the soluble calcium, when represented as a percentage of the total calcium, shows a decrease with increasing age of the leaves.

The soluble magnesium when represented as a percentage of the total magnesium is least when the leaves are full sized but thin. Calculations of the percentage of total magnesium, sodium, and potassium present in the total ash show the usual decrease with increasing age, as found by KELLEY and CUMMINS. The soluble sodium, as a percentage of the total sodium present, decreases with increasing age of the leaves. Over 90 per cent of the total potassium is water-soluble. The percentage of water-soluble phosphorus decreased with increasing age of the leaves, but the percentage of insoluble phosphorus remained practically the same at the different ages.

The results for normal Navel and Valencia orange leaves are

given in table II. In contrast, the results for lemon leaves (table I) take on added importance. The percentage of ash from the water-soluble fraction of mature Navel and Valencia leaves is much higher than that of mature lemon leaves, while the converse is true of the percentage of ash from the insoluble fraction. The water-insolubility of the inorganic constituents of the lemon leaves, when full sized but thin, is greater than for Navel or Valencia orange leaves of the same stage of development. The data given for mature leaves of both varieties are typical of numerous determinations.

The calcium of the mature orange leaves in table II is of special interest, in that about 46–49 per cent of the total calcium of the dry matter is water-soluble, quite in contrast with the value of 17 per cent for mature lemon leaves. The percentages of soluble sodium and phosphorus and insoluble phosphorus decrease with increasing age of the leaves. There is no sharp distinction between the results obtained for Navel and for Valencia orange leaves. It is of additional interest to find, by calculation from the data given, that the soluble calcium as a percentage of the ash of the soluble fraction varies inversely with the values obtained for potassium.

The results presented emphasize the fact that ash analyses of normal citrus leaves, when supplemented with water-solubility data, may give us a dynamic conception of the inorganic constituents instead of a static one. The large water-solubility of the potassium in citrus leaves and the different degrees of solubility of the calcium may throw new light on the mottle-leaf problem.

The function of the large amount of soluble salts in mature Navel and Valencia orange leaves, in contrast with the lower amount in mature lemon leaves, may be of significance during severe desiccating winds, especially during the night time. It has been shown by HAAS and REED (1) that the increased calcium in Valencia orange leaves subject to desiccating winds is represented almost entirely by water-soluble calcium. It is of added interest now to determine what lemon leaves would do with an increased supply of calcium, in view of their normal maintenance of a low solubility for calcium. The use the various citrus leaves make of an insufficient supply of calcium becomes of great importance. The large differences between the soluble calcium of normal mature lemon and orange leaves may

TABLE II

WATER-SOLUBILITY OF DRY MATTER OF NORMAL NAVEL AND VALENCIA ORANGE LEAVES OF DIFFERENT AGES, EXPRESSED AS PERCENTAGES DRY MATTER

Locality (Rubidoux tract)	Age	No. of leaves	Weight		H_2O content as percentage fresh weight	Ash of		Calcium		Soluble as percentage of total	Magnesium		Soluble as percentage of total	Soluble as percentage of total sodium	Soluble as percentage of total potassium	Phosphorus	
			Fresh gm.	Dry gm.		Soluble fraction	Insoluble fraction	Soluble	Insoluble		Soluble	Insoluble				Soluble	Insoluble
	Collected June 22, 1927																
Plot B, Navel	Young	326	60	15	75.00	5.18	2.02	0.553	0.614	47.38	0.216	0.084	72.00	85.44	98.03	0.351	0.069
	Full sized, thin	188	97	24	75.26	4.55	2.69	0.384	0.870	30.62	0.193	0.098	66.32	83.07	97.86	0.283	0.045
	Mature	100	92	40	56.52	7.84	7.10	2.318	2.664	46.53	0.206	0.051	80.16	82.45	97.19	0.098	0.033
Plot B, Valencia	Young	300	42	12	71.43	5.60	2.17	0.904	0.672	57.36	0.180	0.073	71.14	81.67	94.63	.....	.....
	Full sized, thin	115	76	21	72.37	5.39	2.98	0.876	1.106	44.20	0.102	0.042	70.83	77.90	97.59	.....	.....
	Mature	100	90	37	58.89	7.66	7.28	2.505	2.626	48.82	0.196	0.056	77.78	68.28	94.39	.....	.....

be a factor in the difference of behavior between the two species as regards sensitivity to toxic agents such as boron, to desiccating winds, and to hardiness. The writer is continuing these most promising lines of investigation.

Summary

1. The ash of normal citrus leaves of the same age shows practically no difference in composition for the citrus varieties examined. When the dry matter of these leaves is extracted with water, the ash and the calcium of the soluble fraction of mature normal Washington Navel and Valencia orange leaves are greater than those of Eureka lemon.

2. The water content of these leaves as a percentage of their fresh weight changes very little until after the leaves have reached their full size and have begun to mature.

3. The percentage of the total magnesium that is water-soluble is usually at a minimum at the time when the leaves have reached their full size and are still thin.

4. The percentage of the total sodium soluble in water decreases with increasing age of the leaves. Over 90 per cent of the potassium of the dry matter of citrus leaves is water-soluble. The water-soluble phosphorus of the dry matter decreases with increasing age of the leaves.

5. The relationship between the calcium nutrition of these citrus varieties and certain physiological characteristics is discussed to show the bearing the present paper has on the future direction of the investigation of citrus nutrition.

CITRUS EXPERIMENT STATION
RIVERSIDE, CALIF.

[*Accepted for publication December 3, 1927*]

LITERATURE CITED

1. HAAS, A. R. C., and REED, H. S., Relation of desiccating winds to fluctuations in ash content of citrus leaves and phenomenon of mottle-leaf. BOT. GAZ. **83**:161–172. 1927.
2. KELLEY, W. P., and CUMMINS, A. B., Composition of normal and mottled citrus leaves. Jour. Agric. Res. **20**:161–191. 1920.
3. REED, H. S., and HAAS, A. R. C., Some relations between the growth and composition of young orange trees and the concentration of the nutrient solution employed. Jour. Agric. Res. **28**:277–284. 1924.

OVERCOMING DELAYED GERMINATION OF NELUMBO LUTEA

JAMES A. JONES

Introduction

In this investigation it was sought to determine the factors involved in the delayed germination of *Nelumbo lutea*. Seeds were obtained from the Terrell Aquatic Farm of Oshkosh, Wisconsin, for the purpose of determining a method of overcoming the delayed germination, and thereby enabling the dealer to guarantee a high percentage of germination to those growing this plant for water gardens and game preserves. OHGA[1] has reported the results of investigations with *Nelumbo nucifera*. Since the coats of the fruits were found to be impervious to water, the fruits were prepared for germination by treating for five hours with concentrated sulphuric acid, followed by washing and drying.

Method

Control seeds were placed in water at a temperature of 15°–20° C. After eighteen months no visible change had been observed, evidently owing to the extremely hard coat typical of the *Nelumbo* seeds. When the seed coats were filed to expose the brown nucellus tissue before soaking in water, without exception they began immediately to absorb water and became swollen. Seeds having their coats broken with a vise and by abrasion with an emery wheel showed similar results when the embryo was not injured.

Since these tests indicated that the cause of delay in germination was the seed coat, seeds were treated by immersing in concentrated sulphuric acid and removed in groups of one hundred seeds, at intervals of one hour, extending to seventy-two hours. Fifty of the seeds in each case were quickly and thoroughly washed in tap water, to prevent heating by the addition of water to the acid-soaked coat; the other fifty seeds in each test were washed in dilute NH_4OH.

[1] OHGA, I., On the longevity of seeds of *Nelumbo nucifera*. Bot. Mag. Tokyo 37:439–444. 1923.

The seeds were then submerged in water in glass jars, at room temperature, and the water changed frequently at first, to prevent it becoming acid from the acid still left in the thick seed covering. Other seeds similarly treated were dried at room temperature and stored for a period of fourteen days before they were allowed to germinate.

Tests were made to determine the effect of low temperature upon the time of germination. Seeds were allowed to remain in air at a temperature of 0°–5.5° C. for twenty-four hours, and others were placed in water and kept at the same temperature for an identical period. These tests were also run for a period of forty-eight and seventy-two hours, after which the seeds were placed in water in glass jars to germinate.

Seeds were allowed to soak in ethyl alcohol and removed at intervals of thirty minutes and the test terminated at six hours. These seeds were washed in tap water as soon as they were removed, and placed in glass jars to germinate.

Results

Seeds when treated with concentrated sulphuric acid for varying lengths of time up to seventy-two hours, and then washed with tap water, showed that the treatment for one hour was of insufficient duration to produce result. Other tests showed 100 per cent germination in nearly every instance. When germination was not complete the cause apparently was defective seeds which showed no signs of life upon examination. The most practical results were produced by treatment for five hours, showing 10 per cent of the seeds germinating in four days and 100 per cent germinating in thirty-four days. Dilute NH_4OH and tap water were equally effective as neutralizing agents. Seeds similarly treated but dried and stored for fourteen days produced parallel germination results. Untreated seeds which were in water for fourteen months and showed no signs of water absorption or germination responded quickly to this treatment. In one instance complete germination resulted in seven days.

The seeds which had been exposed to low temperature, in both the dry state and in water, showed no seeds swelling or germinating after remaining in water in glass jars for fourteen months.

No germination results were produced from seeds treated with

ethyl alcohol and washed with tap water, although they were kept in correct germinating condition for eighteen months. VERSCHAFFELT[2] has found that water fails to enter the seeds of legumes because it will not wet the walls of the micropyles, but if the seed is first soaked for an hour in ethyl alcohol, it readily enters the openings and furnishes a path for the inward diffusion of water.

Discussion

Although the surface of the testa of the seeds of *Nelumbo lutea* contains many small pores, in the outer walls of the seeds a part of the cellulose has been converted into suberin, which is waterproof and brownish in color. EWART[3] has found that in some hard seeds all layers of the integument are highly impervious to water, and GUPPY[4] claims that this is prevalent among hard-coated forms with large seeds.

It has been shown that the embryos are not dormant, and that germination can be produced by mechanical weakening of the seed coat.

Summary

1. In spite of the presence of a large number of small pores in the seed coat, the seeds of *Nelumbo lutea* did not absorb water and germinate, even after eighteen months' soaking at room temperature.

2. When the seed coats were broken without injuring the embryos, the seeds germinated without exception.

3. Seeds may be prepared for germination by treatment for five hours with concentrated sulphuric acid, following by thorough washing in tap water and later by drying on a screen to eliminate immediate germination. Seeds so treated may be stored by the commercial grower and shipped dry as ordered.

This work has been done under the direction of Dr. J. F. GROVES of Ripon College.

RIPON COLLEGE
RIPON, WIS.

[2] VERSCHAFFELT, E., Rec. Trav. Bot. Neerland **9**:401. 1912.

[3] EWART, A. J., On the longevity of seeds. pp. 210. Victoria, Australia. 1908.

[4] GUPPY, H. B., Studies in seeds and fruits. pp. 585. London. 1912.

[*Accepted for publication October 7, 1927*]

STIMULATING EFFECT OF AMINO ACIDS ON SUGAR METABOLISM OF PLANT AND ANIMAL CELLS

W. E. Burge, G. C. Wickwire, A. M. Estes, and Maude Williams

(with one figure)

Lavoisier (1) found that the ingestion of food increased oxidation or metabolism in the animal. Rubner (3) showed that meat or protein increased metabolism more than did fat or carbohydrate. Lusk (2) found that the amino acids increased metabolism or heat production, and since protein is presented to the tissues of animals as amino acids, the stimulating effect of protein is in reality due to the amino acids. Spoehr and McGee showed that glycine increased sugar utilization by *Helianthus* (4).

The object of this investigation was to determine the effect of optically active and optically inactive amino acids on the sugar metabolism of the plant cell, *Spirogyra porticalis*, and the animal cell, *Paramecium caudatum*. The spirogyra grew in large quantities and fairly pure cultures in a near-by lake. The paramecia were grown in large numbers on an infusion made of lake water and alfalfa. They were collected and washed free of débris with the use of a small centrifugalizing machine. The centrifugalizing tubes were graduated in centimeters, so that the paramecia were measured as they were collected. Air was kept continuously bubbling through the liquid containing the paramecia to insure an adequate supply of oxygen. Dextrose, levulose, and galactose were the sugars used. Sugar determinations were made according to the method of Benedict. The optically active amino acids used were l-leucine, l-tyrosine, l-aspartic acid, l-histidine, d-glutamic acid, l-tryptophan, aminoids; the optically inactive ones were dl-alanine, dl-isoleucine, glycine, dl-phenylalanine, dl-norleucine, dl-leucine, and dl-valine.

The following is the description of a typical experiment. Seventy-five cc. of paramecia was collected, washed, and measured as described, and then introduced into 1500 cc. of aerated lake water, to

which was added 1500 mg. of dextrose. After the sugar was dissolved, this 1500 cc. of paramecia-sugar preparation, while being thoroughly mixed by pouring from one vessel to another, was separated into 100 cc. batches. Each 100 cc. portion was introduced into a 200 cc. sedimentation glass, and air was bubbled through it to insure an adequate supply of oxygen to the paramecia. One hundred mg. of each of the amino acids was introduced into beakers and 10 cc. water added and heated. A sufficient quantity of a saturated solution of sodium bicarbonate was added to form the sodium salts of the acids. Each of these 10 cc. solutions was added to 100 cc. of sugar-paramecia preparation, and 10 cc. of water was added to the controls. Sugar determinations were made immediately and subsequently at intervals. Spirogyra sugar preparations were made as follows. A large batch of spirogyra was collected, brought to the laboratory, and the excess of water removed by gently squeezing with the hands. This large batch was then divided into batches of 40 gm. each. These were then introduced into 200 cc. of 0.1 per cent dextrose solutions in flat bottom dishes 16 cm. in diameter. The sodium salts of the different amino acids were prepared and added as in the paramecia-sugar preparation, and sugar determinations were made immediately and subsequently at intervals. The results of the average of five experiments for spirogyra and five for paramecia are shown in fig. 1. It will be seen that the optically inactive amino acids did not increase the sugar metabolism in either paramecium or spirogyra over the controls, whereas the optically active amino acids produced a great increase in sugar metabolism in both the spirogyra and the paramecium. It may be seen further that the aminoids increased sugar metabolism both in the paramecium and spirogyra. The aminoids were a commercially prepared meat digest containing the naturally occurring amino acids, biuret-free, with a total nitrogen of 10.93 per cent, and the amino nitrogen 75 per cent of the total nitrogen.

Experiments were carried out using levulose and galactose, similar to those in which dextrose was used, with fairly comparable results. Paramecium used all three of the sugars more rapidly than the spirogyra, in keeping with the fact that the metabolic rate of the plant is less intense than that of the animal. It was found also that

paramecium as well as spirogyra used dextrose and levulose more rapidly than galactose, just as is the case with the higher animals and man. It was also found that insulin increased the rate of utilization of these sugars, both by the spirogyra and the paramecium, again resembling the higher animals and man.

It is recognized that optical activity plays a rôle in the plant kingdom. Yeast, for example, will use the dextrorotatory form of

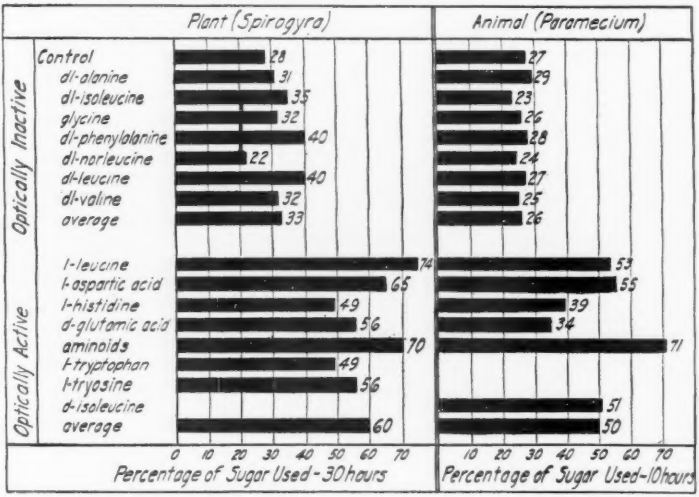


FIG. 1.—Chart showing that optically active amino acids increase rate of sugar utilization in spirogyra and paramecium, whereas optically inactive amino acids do not.

glucose but not the levorotatory form, so if yeast be added to a mixture of dextrorotatory and levorotatory glucose, it will use the dextrorotatory and leave the levorotatory. This is one method of separating these two forms of sugar. It is also known that practically all of the naturally occurring amino acids, and hence the ones normally used, are optically active. The observation reported in this paper, that only the optically active amino acids stimulate metabolism, would seem to attach significance to the fact that with one exception all the naturally occurring amino acids are optically active.

1. The optically active amino acids stimulate sugar metabolism

Summary

in the plant cell, spirogyra, and the animal cell, paramecium, while the optically inactive ones do not.

2. Paramecium uses sugar much more rapidly than spirogyra, in keeping with the more intense metabolism in animals than in plants.

3. Spirogyra and paramecium use dextrose and levulose more rapidly than galactose, just as is the case with higher animals and man.

4. Insulin increases the rate of utilization of the sugars in paramecium and spirogyra, similar to its action in the higher animals and man.

UNIVERSITY OF ILLINOIS
URBANA, ILL.

[*Accepted for publication November 11, 1927*]

LITERATURE CITED

1. LAVOISIER, A. L., Mémoire sur la Chaleur. Mém. Acad. Sci. pp. 355–424. 1780.
2. LUSK, G., The influence of the ingestion of amino acids upon metabolism. Jour. Biol. Chem. **13**:27–155. 1912–13.
3. RUBNER, M., Die Gesetze des Energieverbrauchs bei der Ernaehrung. pp. 322–323. 1902.
4. SPOEHR, H. A., and MCGEE, J. M., Studies in plant respiration and photosynthesis. Carnegie Inst. Wash. Publ. no. 325. pp. 43–44. 1923.

CURRENT LITERATURE

BOOK REVIEWS

Notable books on algae

Three books on algae have recently appeared which will be of use to all interested in this group of plants.

WEST's volume[1] on British freshwater algae, which appeared in 1904, made a place for itself, not only in England but throughout the world; for algae are so cosmopolitan that the book was nearly as useful for ponds about Chicago as for ponds about London. The edition was exhausted even before the death of the author, who was collecting material, notes, and illustrations for a more extensive treatment of the group. At his untimely death the work was still far from the publication stage, but it probably represents much that he had in mind for the new work. This may be due, in considerable measure, to Dr. NELLIE CARTER, who for several years was associated with Professor WEST in his algological studies, and to whom FRITSCH makes acknowledgments for the discussion of many difficult points. Much of the most valuable part of the first edition has been preserved, especially the descriptions of genera and the notes on occurrence and distribution. Some material has been omitted, but much more has been added, so that the size and scope of the work have been increased.

The first 50 pages deal with biology and general features of life histories and development. While the rest of the book is arranged taxonomically and contains the taxonomic keys, it is full of biological notes and descriptions of life histories; so that, in its method of treatment, it lies between such a taxonomic account as we find in ENGLER'S *Pflanzenfamilien* and a morphological biological account like that of OLTMANNS. The directions for collecting algae, keeping them alive in the laboratory, and for making cultures will be useful.

While little attention is paid to alternation of generations, the remark is made that as far as one accepts the diploid and haploid condition as representing alternating generations, "most sexually reproducing freshwater algae may be said to show slight indications of antithetic alternation of generations." The reviewer believes that the algae show the origin of alternation of generations, and, therefore, the true nature of this phenomenon. Plants below the level of sexuality have only one generation, the x, or haploid. The diploid phase arose by the fusion of gametes, and, consequently, must be present not only in "most sexually reproducing freshwater algae," but in all plants and animals which have

[1] WEST, G. S., and FRITSCH, F. E., A treatise on the British freshwater algae. 8vo. pp. xvi+534. *figs. 207*. Cambridge University Press. 1927.

sexuality. If the zygote divides several times before reduction of chromosomes takes place, it builds up a more or less conspicuous diploid generation; but even when the reduction of chromosomes takes place during the first two divisions of the zygote, as in *Spirogyra* and all the rest of the Chlorophyceae which have been examined, the diploid generation has been started. If, in *Coleochaete*, the reduction should not be completed until the 16-cell stage has been reached, there would be a diploid body which would be recognized as comparable with that of *Riccia*. Logically, it makes no difference whether there are 50 mitoses, or whether there are 25, 10, or only the two which are necessary to bring the plant back to the original haploid condition. Much confusion has arisen from the assumption that haploid generation and gametophyte generation are synonymous terms, and that diploid generation means the same as sporophyte generation. From the liverworts to the orchids and in many thallophytes the terms are synonymous; but in many thallophytes, where alternation is originating and becoming established, the terms are not synonymous.

It has long been recognized that it is difficult to separate the algae from the pigmented Flagellates. OLTMANNS began his book on the *Morphologie und Biologie der Algen* with the statement that the algae go back, phylogenetically, to the Flagellates; and this view has become a conviction with most students of algae. It was the fact that many Flagellates are just as distinctly animals as others are distinctly plants that led some zoologists to regard the Volvocales as animals because they are obviously related to the Flagellates. The present volume, by including the pigmented Flagellates in a textbook treatise on algae, will bring this group to the attention of a large number of teachers who are not specialists in algae, and thus lead to a better understanding of the Volvocales.

Morphologists and cytologists will readily agree that the diatoms should not be associated with the Phaeophyceae; but they will not so readily agree that they should be removed from their association with the desmids and the rest of that group. I should not agree that the evidence for placing the diatoms in the Zygophyceae is superficial; it is strictly internal.

The Cyanophyceae are placed at the end of the book. If they are to be included in the algae at all, their simple nuclear structure and the fact that not a single one of them has reached the level of sexuality might give them a place even lower than the Flagellates.

The artificial keys and the arrangement of material give the book a taxonomic aspect, and make it easy to find data in regard to any particular form; but, besides the descriptions of families, genera, and species, there are special accounts of distribution, structure, development, and the biology of life histories, in addition to the general accounts given in the first 50 pages.

Unless the present edition is much larger than the previous one, it will soon be exhausted. There is need for a similar account in English, including the algae of the world, both freshwater and marine.

PASCHER'S[2] immense work on the freshwater flora of Germany, Austria, and Switzerland is progressing. The volume on the Cyanophyceae, by GEITLER, has already been noted in this journal.[3] The present work, Volume IV, by PASCHER himself, is devoted entirely to the Volvocales, with the exception of a few pages of general introduction to the Chlorophyceae. It is the first comprehensive treatment of this important order.

The book should be regarded as a taxonomic monograph of the Volvocales, but it is more than an assemblage of taxonomic keys. The descriptions are very thorough, with discussions of relationships and some attention to biological conditions; but the taxonomic feature is dominant, just as the biological and morphological features are dominant in the work of WEST and FRITSCH. The synonomy is everywhere very complete. *Chlamydomonas* may be taken as an example. More than three pages are devoted to the synonomy and diagnosis of the genus, and 132 pages are devoted to keys and detailed descriptions of the 146 recognized species, and three pages more to doubtful species. Illustrations of critical features add to the value of the diagnoses.

It is fortunate that one so thoroughly acquainted with the Volvocales has devoted so much space to a description of the more difficult lower members of the order. This treatment will enable those who are not specialists to understand something of the relationships of the Volvocales to the Flagellates and to other groups.

A volume by MELCHIOR[4] on the algae covers the Cyanophyceae, Flagellatae, Dinoflagellatae, and Bacillariales. It is the first volume of a series presenting all the algae, and is the second and much enlarged edition of the book by LINDAU, who outlined a complete series dealing with all the Cryptogams, under the title *Kryptogamenflora für Anfänger*. While the treatment is not so detailed as in PASCHER'S work, it would look rather difficult for a beginner. After about 40 pages of introduction, the rest of the book is strictly taxonomic, with keys in German, as in the PASCHER series.

The fact that these three major books have appeared within a year indicates an interest in the lower Cryptogams.—C. J. CHAMBERLAIN.

An introductory botany

A textbook by TORREY[5] dealing with introductory botany deserves the consideration of teachers, since the author has definite and pronounced views in regard to the teaching of this subject. He is clearly of the opinion that a serious

---

[2] PASCHER, A., Die Süsswasser-Flora Deutschlands, Oesterreichs und der Schweiz. Heft 4: Volvocales. 8vo. pp. vi+506. *figs. 451*. Jena: Gustav Fischer. 1927.

[3] BOT. GAZ. 82:341. 1926.

[4] MELCHIOR, HANS, Die Algen, Erste Ableilung. 8vo. pp. viii+314. *figs. 489*. Berlin: Julius Springer. 1926.

[5] TORREY, R. E., Introductory botany, 2d ed. Vol. I: Structure and classification of seed plants. pp. xvii+141. *figs. 77;* Vol. II: The anatomy and physiology of seed plants. pp. viii+127. *figs. 71*. Mass. Agric. Coll. Book Store. 1926. $1.65 and $1.35.

effort should be made to reconcile the purely inductive and the philosophical points of view in the teaching of botanical science to beginners. There can be no doubt that he is largely right in this attitude, because the results of the purely inductive method are certainly discouraging from the standpoint of enlightened pedagogy. The book under discussion makes a happy compromise between the narrowness of the mere observationist and the too comprehensive superficiality of the purely philosophical mind.

The author intersperses his descriptions of the various aspects of the subject which he treats with pregnant and forceful phrases, which should serve as vigorous mental stimulants to the classes who are fortunate enough to make use of this new textbook. Many of the illustrations are original, and show not only good technique but admirable judgment in the matter of utility. Since the author adopts a general point of view, he is always at pains to connect his facts with an interesting train of reasoning. In this connection it may be remarked that the present work is the only one which embodies recent results in the evolution of the various elements and organs of woody plants. The treatment of the origin of the herbaceous dicotyledonous and monocotyledonous types is particularly happy, and illustrated by original drawings which serve to illuminate an important subject particularly difficult to the beginner. The author makes very clear the importance of the herbaceous type in connection with the sustenance of the human species. The subjects of taxonomy, paleobotany, plant physiology, ecology, evolution, etc., are also handled in an illuminating fashion and with excellent judgment, and in such a way as to inspire interest in students whose mental processes are in any way active.

The publication of this excellent work in two small volumes under State auspices has in all probability stood in the way of its adoption by a wider range of colleges. The author, however, has made a distinct contribution to biological pedagogy in the way of a new method of teaching essential structures. One of the bugbears of biology has been the making of endless drawings in the laboratory. This has militated against the popularity of the subject with the beginner, even at a time when biology has again entered the position of controversial interest which it occupied so brilliantly two generations ago. TORREY has attempted to meet this difficulty by providing line reproductions of drawings, on a sufficient scale of enlargement for the student to recognize and label the parts, whether gross and superficial or minute and microscopical, accurately and with comprehension. This is a distinct advance pedagogically, and seems to present advantages from the standpoint of elementary instruction. It may be added that TORREY'S method has been tried out with success in the botanical portion of a cultural course in Harvard University. It is to be noted that the same method of treatment has been more recently adopted in zoology. In conclusion, one may remark that in this book we have a concise, interesting, well planned, and decidedly novel presentation of the subject, which will probably meet the needs of many teachers who are dissatisfied with the books at present available for elementary instruction in botany.—E. C. JEFFREY.

NOTES FOR STUDENTS

Accuracy of measuring concentration of hydrogen ions.—Since 1920, when BIILMANN described his quinhydrone electrode, this method has been more and more adopted in measuring the hydrogen ions in soils. The hydrogen electrode is now but little used in such researches, owing to the length of time and trouble involved in the measurements. The quinhydrone method and the colorimetric method are now chiefly employed. As regard the accuracy of the two methods, there seems to be a difference of opinion.

With a view to ascertaining the degree of accuracy attainable in measuring the hydrogen ion concentration of soils, OLSEN and LINDERSTRM-LANG[6] made a thorough investigation of the different methods.

Measurement with the hydrogen electrode has been regarded as a standard method, with which values found by the other two methods may be compared. However, the ordinary hydrogen electrode values cannot be used for comparison where the pH value of the soil exceeds about 5.0, as the carbonic acid is gradually given off in the course of measurement and the pH value is altered.

From investigations including measurements of 100 soil samples the quinhydrone electrode gave, in some cases, a value 0.8 too high, and it is impossible to introduce any correction for this. In the colorimetric method a correction can be introduced, and when this is done the pH values of soil samples can be measured with an accuracy of ± 0.15 pH. In general, soils cannot be measured more accurately than this. In the great majority of cases this will be quite sufficient in soil investigations, as the organisms of the soil are not appreciably sensitive to small differences in pH.—J. ISENBARGER.

An illustrated flora of China.—HU and CHUN[7] of the National Southeastern University at Nanking, China, have published the first fascicle of a remarkably elaborate presentation of the plants of China. The large size (48×31 cm.) makes the handsome plates unusually impressive. This first fascicle is dedicated to CHARLES S. SARGENT, in memory of his interest in the woody flora of China. Fifty species are described, in 39 genera, in both English and Chinese, with the facts of distribution and a general account of habitats and uses. Most of them are woody plants, the largest group being the Coniferae. The plates are so large and well prepared that they seem almost as effective as herbarium specimens.—J. M. C.

---

[6] OLSEN, C., and LINDERSTRM-LANG, K., On the accuracy of the various methods of measuring concentration of hydrogen ions in soil. Compt. Rend. Travaux Laboratorie Carlsberg. **17**: no. 1. 1927.

[7] HU, HSEN-HSU, and CHUN, WOOD-YOUNG, Icones Plantarum Sinicarum. Fascicle I. pp. 50. *pls.* 50. 1927.

Cambridge University Press

The Structure and Development of the Fungi. By H. C. I. GWYNNE-VAUGHAN, D.B.E., and B. BARNES, B.Sc. With a frontispiece and 285 text-figures. Demy 8vo. $4.25.

A Treatise on the British Freshwater Algae. By G. S. WEST, M.A., D.Sc. (New Edition re-written by F. E. FRITSCH.) Demy 8vo. $7.00.

The Ferns (Filicales). By F. O. BOWER, Sc.D., LL.D., F.R.S. Vol. I. Analytical Examination of the Criteria of Comparison. With 310 illustrations. Royal 8vo. $10.00. Vol. II. The Eusporangiatae and Other Relatively Primitive Ferns. With 276 illustrations. Royal 8vo. $10.00.

The Classification of Flowering Plants. By A. B. RENDLE, M.A., D.Sc., F.R.S. Vol. I. Gymnosperms and Monocotyledons. With 187 illustrations. Demy 8vo. $7.00. Vol. II. Dicotyledons. With 279 illustrations. Demy 8vo. $10.50. (*Biological Series.*)

A Dictionary of the Flowering Plants and Ferns. By J. C. WILLIS, M.A., Sc.D., F.R.S. Fifth Edition, revised and re-written. Crown 8vo. $8.00. (*Biological Series.*)

Inorganic Plant Poisons and Stimulants. By W. E. BRENCHLEY, D.Sc. With 19 illustrations. Second Edition. Royal 8vo. $3.50.

Devonian Floras. A Study of the Origin of Cormophyta. By E. A. N. ARBER, Sc.D. Preface by D. H. SCOTT, LL.D., Ph.D., F.R.S. With a frontispiece and 47 text-figures. Demy 8vo. $6.00.

Fossil Plants. A Text-book for Students of Botany and Geology. By A. C. SEWARD, Sc.D., F.R.S. 4 Vols. Demy 8vo. Vol. I. With 112 illustrations. *Out of print.* Vol. II. With 266 illustrations. $9.00. Vol. III. With 254 illustrations. $8.75. Vol. IV. With 190 illustrations. $8.75. (*Biological Series.*)

Water Plants. A Study of Aquatic Angiosperms. By A. ARBER, D.Sc., F.L.S. With 172 illustrations. Royal 8vo. $10.50.

Monocotyledons. By A. ARBER, M.A., D.Sc. With 161 illustrations. Royal 8vo. $7.00.

Age and Area. A Study in Geographical Distribution and Origin of Species. By J. C. WILLIS, M.A., D.Sc. With chapters by H. DE VRIES, H. B. GUPPY, MRS. E. M. REID, and J. SMALL. With tables and diagrams. Demy 8vo. $5.00.

The Elements of Botany. By SIR F. DARWIN, Sc.D., M.B., F.R.S. Second Edition. With 94 illustrations. Crown 8vo. $2.60. (*Biological Series.*)

Published by the Cambridge University Press (England)
Sold by The Macmillan Company, Agents in the United States
60 Fifth Avenue, New York City

AMERICAN JOURNAL OF BOTANY

Devoted to All Branches of Botanical Science

Established 1914. Monthly, except August and September. Official publication of the Botanical Society of America. Subscription, $7 a year for complete volumes (January-December). Parts of volumes are to be had only at the single number rate. Volumes 1–14 complete, $114. Single numbers, $1.00 each, post free. Prices of odd volumes on request. Foreign postage: 40 cents.

ECOLOGY

Devoted to All Forms of Life in Relation to Environment

Established 1910. Quarterly. Official Publication of the Ecological Society of America. Subscription, $4 a year for complete volumes (January-December). Parts of volumes are to be had at the single number rate. Back volumes 1, 2, and 4–8, $5.00 each. Single numbers, $1.25 post free. Foreign postage: 20 cents.

GENETICS

A Periodical Record of Investigations Bearing on Heredity and Variation

Established 1916. Bimonthly. Subscription, $6 a year for complete volumes (January-December). Parts of volumes are to be had only at the single number rate. Single numbers, $1.25 post free. Back volumes 2, 3, and 5–12 only, $7.00 each. Foreign postage: 50 cents.

BROOKLYN BOTANIC GARDEN MEMOIRS

Volume I: 33 contributions by various authors on genetics, pathology, mycology, physiology, ecology, plant geography, and systematic botany. Price $3.50 plus postage.

Volume II: The vegetation of Long Island. Part I, The vegetation of Montauk, etc. Pub. 1923. 108 pp. Price, $1.

Volume III: The vegetation of Mt. Desert Island, Maine, and its environment. By Barrington Moore and Norman Taylor. 151 pp., 27 text-figures, Vegetation map in colors. Published June 10, 1927. Price $1.60.

Orders should be placed with

THE SECRETARY, BROOKLYN BOTANIC GARDEN
1000 WASHINGTON AVE. BROOKLYN, N.Y., U.S.A.

THE GENUS IRIS

By WILLIAM R. DYKES

This work brings together the available information on all known species of Iris. It describes each plant, gives observations on its peculiarities, its position in the genus, its value as a garden plant, and discusses its cultivation.

Forty-seven life-size colored plates and thirty line drawings illustrate the work. (Published by the Cambridge University Press, London.)

254 pages, demy folio, half morocco, $58.50, postage extra

Order from

THE UNIVERSITY OF CHICAGO PRESS
CHICAGO · ILLINOIS